

NOAA Technical Report NMFS Circular 445



Sharks of the Genus *Carcharhinus*

J. A. F. Garrick

May 1982

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

57758 403A

NOAA TECHNICAL REPORTS

National Marine Fisheries Service, Circulars

The major responsibilities of the National Marine Fisheries Service (NMFS) are to monitor and assess the abundance and geographic distribution of fishery resources, to understand and predict fluctuations in the quantity and distribution of these resources, and to establish levels for optimum use of the resources. NMFS is also charged with the development and implementation of policies for managing national fishing grounds, development and enforcement of domestic fisheries regulations, surveillance of foreign fishing off United States coastal waters, and the development and enforcement of international fishery agreements and policies. NMFS also assists the fishing industry through marketing service and economic analysis programs, and mortgage insurance and vessel construction subsidies. It collects, analyzes, and publishes statistics on various phases of the industry.

The NOAA Technical Report NMFS Circular series continues a series that has been in existence since 1941. The Circulars are technical publications of general interest intended to aid conservation and management. Publications that review in considerable detail and at a high technical level certain broad areas of research appear in this series. Technical papers originating in economics studies and from management investigations appear in the Circular series.

NOAA Technical Report NMFS Circulars are available free in limited numbers to governmental agencies, both Federal and State. They are also available in exchange for other scientific and technical publications in the marine sciences. Individual copies may be obtained from D822, User Services Branch, Environmental Science Information Center, NOAA, Rockville, MD 20852. Recent Circulars are:

418. Annotated bibliography of four Atlantic scombrids: *Scomberomorus brasiliensis*, *S. cavalla*, *S. maculatus*, and *S. regalis*. By Charles S. Manooch III, Eugene L. Nakamura, and Ann Bowman Hall. December 1978, iii + 166 p.
419. Marine flora and fauna of the northeastern United States. Protozoa: Sarcodina: Amoeboae. By Eugene C. Bovee and Thomas K. Sawyer. January 1979, iii + 56 p., 77 figs.
420. Preliminary keys to otoliths of some adult fishes of the Gulf of Alaska, Bering Sea, and Beaufort Sea. By James E. Morrow. February 1979, iii + 32 p., 9 pl.
421. Larval development of shallow water barnacles of the Carolinas (Cirripedia: Thoracica) with keys to naupliar stages. By William H. Lang. February 1979, iv + 39 p., 36 figs., 17 tables.
422. A revision of the catsharks, family Scyliorhinidae. By Stewart Springer. April 1979, v + 152 p., 97 figs.
423. Marine flora and fauna of the northeastern United States. Crustacea: Cumacea. By Les Watling. April 1979, iii + 23 p., 35 figs.
424. Guide to the leptocephali (Elopiformes, Anguilliformes, and Notacanthiformes). By David G. Smith. July 1979, iv + 39 p., 54 figs.
425. Marine flora and fauna of the northeastern United States. Arthropoda: Cirripedia. By Victor A. Zullo. April 1979, iii + 29 p., 40 figs.
426. Synopsis of biological data on the rock crab, *Cancer irroratus* Say. By Thomas E. Bigford. May 1979, v + 26 p., 11 figs., 21 tables.
427. Ocean variability in the U.S. Fishery Conservation Zone, 1976. By Julien R. Goulet, Jr. and Elizabeth D. Haynes, editors. July 1979, iii + 362 p.
428. Morphological comparisons of North America sea bass larvae (Pisces: Serranidae). By Arthur W. Kendall, Jr. August 1979, iv + 50 p., 43 figs., 9 tables, 1 app. table.
429. Synopsis of biological data on tunas of the genus *Euthynnus*. By Howard O. Yoshida. October 1979, iv + 57 p., 40 figs., 30 tables.
430. Guide to identification of some sculpin (Cottidae) larvae from marine and brackish waters off Oregon and adjacent areas in the northeast Pacific. By Sally L. Richardson and Betsy B. Washington. January 1980, iv + 56 p., 32 figs., 45 tables.
431. Guide to some trawl-caught marine fishes from Maine to Cape Hatteras, North Carolina. By Donald D. Flescher. March 1980, iii + 34 p., illustrations.
432. Synopsis of biological data on bonitos of the genus *Sarda*. By Howard O. Yoshida. May 1980, iv + 50 p., 26 tables, 43 figs.
433. Synopsis of biological data on striped bass, *Morone saxatilis* (Walbaum). By Eileen M. Setzler, Walter R. Boynton, Kathryn V. Wood, Henry H. Zion, Lawrence Lubbers, Nancy K. Mountford, Phyllis Frere, Luther Tucker, and Joseph A. Mihursky. June 1980, v + 69 p., 9 figs., 24 tables.
434. Osteology, phylogeny, and higher classification of the fishes of the order Plectognathi (Tetraodontiformes). By James C. Tyler. October 1980, xi + 422 p., 326 figs., 3 tables.
435. Field guide to fishes commonly taken in longline operations in the western North Atlantic Ocean. By Joseph L. Russo. January 1981, iii + 51 p., 2 figs. + illusts.
436. Synopsis of biological data on frigate tuna, *Auxis thazard*, and bullet tuna, *A. rochei*. By Richard N. Uchida. January 1981, iv + 63 p., 52 figs., 27 tables.

NOAA Technical Report NMFS Circular 445

Sharks of the Genus *Carcharhinus*

J. A. F. Garrick

May 1982



U.S. DEPARTMENT OF COMMERCE

Malcolm Baldrige, Secretary

National Oceanic and Atmospheric Administration

John V. Byrne, Administrator

National Marine Fisheries Service

William G. Gordon, Assistant Administrator for Fisheries

The National Marine Fisheries Service (NMFS) does not approve, recommend or endorse any proprietary product or proprietary material mentioned in this publication. No reference shall be made to NMFS, or to this publication furnished by NMFS, in any advertising or sales promotion which would indicate or imply that NMFS approves, recommends or endorses any proprietary product or proprietary material mentioned herein, or which has as its purpose an intent to cause directly or indirectly the advertised product to be used or purchased because of this NMFS publication.

CONTENTS

Introduction	1
Materials	2
Methods	3
Measurements	3
Counts	3
Teeth	3
Vertebrae	3
Consideration of some characters used in this study	3
Morphometrics	3
Vertebrae	9
Teeth	12
Middorsal dermal ridge	13
Color	15
Dermal denticles	18
Biology	18
Generic synonymy	19
Generic diagnosis	20
Intrageneric relationships of <i>Carcharhinus</i> species	20
Some species groups	20
<i>limbatus-amblyrhynchoides</i> group	22
<i>sealei-dussumieri</i> group	22
<i>leucas-amboinensis</i> group	23
<i>melanopterus-cautus</i> group	23
<i>amblyrhynchos-wheeleri</i> group	23
<i>obscurus-galapagensis</i> group	23
Other species and possible relationships	23
<i>falciformis</i> and <i>sorrah</i>	23
<i>brachyurus</i>	24
<i>borneensis</i>	24
<i>Carcharhinus</i> species and their primary synonyms	24
Key to the species of <i>Carcharhinus</i>	25
Species accounts	28
<i>Carcharhinus limbatus</i>	28
<i>Carcharhinus amblyrhynchoides</i>	37
<i>Carcharhinus brevipinna</i>	41
<i>Carcharhinus sealei</i>	48
<i>Carcharhinus dussumieri</i>	54
<i>Carcharhinus acronotus</i>	65
<i>Carcharhinus porosus</i>	69
<i>Carcharhinus fitzroyensis</i>	78
<i>Carcharhinus leucas</i>	81
<i>Carcharhinus amboinensis</i>	91
<i>Carcharhinus melanopterus</i>	96
<i>Carcharhinus cautus</i>	102
<i>Carcharhinus amblyrhynchos</i>	106
<i>Carcharhinus wheeleri</i>	111
<i>Carcharhinus albimarginatus</i>	116
<i>Carcharhinus obscurus</i>	120
<i>Carcharhinus galapagensis</i>	126
<i>Carcharhinus plumbeus</i>	132
<i>Carcharhinus altimus</i>	142
<i>Carcharhinus perezii</i>	145
<i>Carcharhinus longimanus</i>	150
<i>Carcharhinus falciformis</i>	159
<i>Carcharhinus sorrah</i>	165
<i>Carcharhinus brachyurus</i>	171
<i>Carcharhinus borneensis</i>	179
Zoogeography of <i>Carcharhinus</i> species	182
Species dubia	185
<i>Carcharias brachyrrhynchus</i> Philippi	185
<i>Eulamia philippi</i> Fowler	185

<i>Prionodon cucuri</i> Castelnau	185
<i>Galeolamna greyi</i> Owen	186
<i>Carcharias falcipinnis</i> Lowe	187
<i>Hypoprion? Hemigaleus? heterodus</i> Philippi	187
<i>Hypoprion? Hemigaleus? isodus</i> Philippi	187
<i>Carcharias Javanicus</i> Van Hasselt	187
<i>Carcharias (Prionodon) munsing</i> Bleeker	187
<i>Carcharias Murrayi</i> Günther	188
<i>Carcharias robustus</i> Philippi	188
<i>Carcharias sancti-thomae</i> Engelhardt	188
<i>Carcharias (Prionodon) siamensis</i> Steindachner	188
<i>Carcharhinus watu</i> Setna & Sarangdhar	189
Acknowledgments	189
Literature cited	189

Plate

1. Radiographs of <i>Carcharhinus</i> species showing variation in the nature of the diplospondylous centra	16
---	----

Figures

1. Examples of measurements made in this study and some terminology of structures	4
2-8. Proportional dimensions of 25 species of <i>Carcharhinus</i>	5-11
9. Relation of mean number of precaudal and caudal vertebrae to maximum total length in 25 species of <i>Carcharhinus</i>	15
10. Length of penultimate monospondylous centrum divided by its diameter in 24 species of <i>Carcharhinus</i>	15
11. Length of penultimate monospondylous centrum divided by length of first diplospondylous centrum in 24 species of <i>Carcharhinus</i>	15
12. Position where diplospondyly begins in 24 species of <i>Carcharhinus</i>	15
13. Number of embryos per litter, size at birth, size at first maturity, and maximum size in 24 species of <i>Carcharhinus</i>	18
14. Relation of median number of embryos per litter to median size at birth as percent of maximum adult size in 21 species of <i>Carcharhinus</i>	19
15. Upper tooth shape as exemplified by fifth upper tooth in 24 species of <i>Carcharhinus</i>	21
16. Atlantic <i>Carcharhinus limbatus</i>	28
17. Pacific <i>Carcharhinus limbatus</i>	29
18. <i>Carcharhinus limbatus</i> teeth	29
19. <i>Carcharhinus amblyrhynchoides</i>	38
20. <i>Carcharhinus amblyrhynchoides</i> teeth	38
21. <i>Carcharhinus brevipinna</i>	41
22. <i>Carcharhinus brevipinna</i> teeth	41
23. Western Pacific <i>Carcharhinus sealei</i>	48
24. Western Indian Ocean <i>Carcharhinus sealei</i>	48
25. <i>Carcharhinus sealei</i> teeth	49
26. Second dorsal height as percent of total length versus total length in <i>Carcharhinus sealei</i>	50
27. Preoral length as percent of total length versus total length in <i>Carcharhinus sealei</i>	50
28. <i>Carcharhinus dussumieri</i>	55
29. <i>Carcharhinus dussumieri</i>	55
30. Variation in snout shape and proportions in <i>Carcharhinus dussumieri</i>	56
31. <i>Carcharhinus dussumieri</i> female teeth	56
32. <i>Carcharhinus dussumieri</i> male teeth	57
33. Proportional dimensions indicating differences between <i>Carcharhinus dussumieri</i> and <i>C. sealei</i>	60
34. <i>Carcharhinus acronotus</i>	65
35. <i>Carcharhinus acronotus</i> teeth	65
36. <i>Carcharhinus porosus</i>	69
37. <i>Carcharhinus porosus</i> teeth	70
38. <i>Carcharhinus fitzroyensis</i>	78
39. <i>Carcharhinus fitzroyensis</i> teeth	79
40. <i>Carcharhinus leucas</i> male	82
41. <i>Carcharhinus leucas</i> teeth	83
42. <i>Carcharhinus amboinensis</i>	92
43. <i>Carcharhinus melanopterus</i>	96
44. <i>Carcharhinus melanopterus</i> teeth	97
45. <i>Carcharhinus cautus</i> late embryo	103

46.	<i>Carcharhinus cautus</i> adult	103
47.	<i>Carcharhinus cautus</i> late embryo teeth	104
48.	<i>Carcharhinus amblyrhynchos</i>	107
49.	<i>Carcharhinus amblyrhynchos</i> teeth	107
50.	<i>Carcharhinus wheeleri</i> n. sp., holotype	112
51.	<i>Carcharhinus wheeleri</i> n. sp., holotype teeth	112
52.	Proportional dimensions indicating differences between <i>Carcharhinus wheeleri</i> n. sp. and <i>C. amblyrhynchos</i>	113
53.	<i>Carcharhinus albimarginatus</i>	117
54.	<i>Carcharhinus albimarginatus</i> teeth	117
55.	<i>Carcharhinus obscurus</i>	121
56.	<i>Carcharhinus obscurus</i> teeth	121
57.	<i>Carcharhinus galapagensis</i>	127
58.	<i>Carcharhinus galapagensis</i> , paratype of <i>Carcharias nesiotes</i>	127
59.	<i>Carcharhinus galapagensis</i> teeth	128
60.	<i>Carcharhinus plumbeus</i>	132
61.	<i>Carcharhinus plumbeus</i> teeth	133
62.	Reproduction of two figures from an unpublished manuscript by Chiereghini in the Marciana Library of Venice	133
63.	First dorsal fin height as percent of total length versus total length in <i>Carcharhinus plumbeus</i>	140
64.	<i>Carcharhinus altimus</i>	142
65.	<i>Carcharhinus altimus</i> teeth	143
66.	<i>Carcharhinus perezii</i>	146
67.	<i>Carcharhinus perezii</i> teeth	146
68.	Reproduction of a tracing from an unpublished drawing labelled <i>Platypodon perezii</i>	147
69.	<i>Carcharhinus longimanus</i>	150
70.	<i>Carcharhinus longimanus</i> teeth	151
71.	Reproduction of illustration which accompanied Lesson's (1830) description of <i>Squalus maou</i>	152
72.	Pattern of growth change in the first dorsal and pectoral fins of <i>Carcharhinus longimanus</i>	154
73.	<i>Carcharhinus falciformis</i>	159
74.	<i>Carcharhinus falciformis</i> teeth	160
75.	<i>Carcharhinus sorrah</i>	165
76.	<i>Carcharhinus sorrah</i> teeth	166
77.	Reproduction of an unpublished drawing by Lesueur labelled " <i>Sq. spalanzani</i> "	166
78.	<i>Carcharhinus brachyurus</i> neotype	172
79.	<i>Carcharhinus brachyurus</i>	172
80.	<i>Carcharhinus brachyurus</i> female teeth	173
81.	<i>Carcharhinus brachyurus</i> mature male teeth	173
82.	<i>Carcharhinus borneensis</i>	179
83.	<i>Carcharhinus borneensis</i> teeth	179

Tables

1.	Total vertebral numbers in 25 species of <i>Carcharhinus</i>	12
2.	Precaudal and caudal vertebral numbers, and maximum total length in 25 species of <i>Carcharhinus</i>	13
3.	Frequency distribution of precaudal vertebral numbers in 25 species of <i>Carcharhinus</i>	14
4.	Frequency distribution of tooth numbers, and commonest dental formula in 25 species of <i>Carcharhinus</i>	17
5.	Occurrence of middorsal dermal ridge in <i>Carcharhinus</i> species	18
6.	Available genus-group names for <i>Carcharhinus</i> species	20
7.	Proportional dimensions showing differences between <i>Carcharhinus limbatus</i> and <i>C. amblyrhynchoides</i>	30
8.	<i>Carcharhinus limbatus</i> , proportional dimensions in percentage of total length	32
9.	Prenarial length as percentage of total length in <i>Carcharhinus limbatus</i>	33
10.	Frequency distribution of precaudal and caudal vertebral numbers in <i>Carcharhinus limbatus</i>	33
11.	Vertebral numbers in 125 specimens of <i>Carcharhinus limbatus</i>	35
12.	Size at birth and number of young per litter in <i>Carcharhinus limbatus</i>	35
13.	<i>Carcharhinus amblyrhynchoides</i> , proportional dimensions in percentage of total length	40
14.	<i>Carcharhinus brevipinna</i> , proportional dimensions in percentage of total length	44
15.	Vertebral numbers in 127 specimens of <i>Carcharhinus brevipinna</i>	46
16.	Frequency distribution of precaudal and caudal vertebral numbers in <i>Carcharhinus brevipinna</i>	46
17.	Size at maturity in the female, and number of young per litter in <i>Carcharhinus brevipinna</i>	47
18.	Proportional dimensions showing differences between two geographically separated groups of <i>Carcharhinus sealei</i>	50
19-20.	<i>Carcharhinus sealei</i> , proportional dimensions in percentage of total length	51-52
21.	Vertebral numbers in 25 specimens of <i>Carcharhinus sealei</i>	53
22.	Proportional dimensions showing differences between <i>Carcharhinus dussumieri</i> and <i>C. sealei</i>	57
23.	Frequency distribution of number of precaudal vertebrae in <i>Carcharhinus dussumieri</i> and <i>C. sealei</i>	58

24.	Frequency distribution of number of monospondylous centra in <i>Carcharhinus dussumieri</i> and <i>C. sealei</i>	58
25.	Vertebral numbers and proportional dimensions used in referring various nominal species to either <i>Carcharhinus dussumieri</i> or <i>C. sealei</i>	58-59
26.	<i>Carcharhinus dussumieri</i> , proportional dimensions in percentage of total length	61
27.	Vertebral numbers in 33 specimens of <i>Carcharhinus dussumieri</i>	63
28.	Clasper length as percentage of total length in <i>Carcharhinus dussumieri</i>	63
29.	Proportional dimensions showing that the holotype of <i>Carcharhinus remotus</i> agrees more closely with specimens of <i>C. acronotus</i> than with specimens of <i>C. remotus</i> sensu Bigelow & Schroeder	68
30.	<i>Carcharhinus acronotus</i> , proportional dimensions in percentage of total length	68
31.	Vertebral numbers in four specimens of <i>Carcharhinus acronotus</i>	69
32.	Proportional dimensions showing differences between Asian and American specimens of <i>Carcharhinus porosus</i>	72
33-34.	<i>Carcharhinus porosus</i> , proportional dimensions in percentage of total length	73-74
35.	Vertebral numbers in 35 specimens of <i>Carcharhinus porosus</i>	75
36.	Frequency distribution of precaudal and caudal vertebral numbers in <i>Carcharhinus porosus</i>	76
37.	Proportional dimensions of penultimate monospondylous centrum and first diplospondylous centrum in 31 specimens of <i>Carcharhinus porosus</i>	76
38.	<i>Carcharhinus fitzroyensis</i> , proportional dimensions in percentage of total length	80
39.	Precaudal vertebral numbers, proportional dimensions, and dental formulae used in referring various nominal species to either <i>Carcharhinus amboinensis</i> or <i>C. leucas</i>	84-85
40.	<i>Carcharhinus leucas</i> , proportional dimensions in percentage of total length	87
41.	Vertebral numbers in 53 specimens of <i>Carcharhinus leucas</i>	89
42.	Precaudal vertebral numbers in <i>Carcharhinus leucas</i> from different localities	89
43.	Clasper length as percentage of total length in <i>Carcharhinus leucas</i>	89
44.	Size of pregnant females, number of embryos per litter, and size of embryos in <i>Carcharhinus leucas</i>	90
45.	Frequency distribution of number of teeth on each side of lower jaw in <i>Carcharhinus amboinensis</i> and <i>C. leucas</i>	93
46.	<i>Carcharhinus amboinensis</i> , proportional dimensions in percentage of total length	95
47.	Vertebral numbers in 18 specimens of <i>Carcharhinus amboinensis</i>	95
48.	<i>Carcharhinus melanopterus</i> , proportional dimensions in percentage of total length	99
49.	Vertebral numbers in 26 specimens of <i>Carcharhinus melanopterus</i>	100
50.	<i>Carcharhinus caudatus</i> , proportional dimensions in percentage of total length	105
51.	Vertebral numbers in four specimens of <i>Carcharhinus caudatus</i>	106
52.	<i>Carcharhinus amblyrhynchus</i> , proportional dimensions in percentage of total length	109
53.	Vertebral numbers in three specimens of <i>Carcharhinus amblyrhynchus</i>	110
54.	Proportional dimensions indicating differences between <i>Carcharhinus wheeleri</i> and <i>C. amblyrhynchus</i>	113
55.	<i>Carcharhinus wheeleri</i> n. sp., proportional dimensions in percentage of total length	115
56.	Vertebral numbers in two specimens of <i>Carcharhinus wheeleri</i>	115
57.	Number of embryos per litter, size at birth, size at maturity, and maximum size of <i>Carcharhinus wheeleri</i>	116
58.	<i>Carcharhinus albimarginatus</i> , proportional dimensions in percentage of total length	119
59.	Vertebral numbers in two specimens of <i>Carcharhinus albimarginatus</i>	120
60.	Proportional dimensions showing differences between <i>Carcharhinus obscurus</i> and <i>C. galapagensis</i>	122
61.	<i>Carcharhinus obscurus</i> , proportional dimensions in percentage of total length	123
62.	Vertebral numbers in 10 specimens of <i>Carcharhinus obscurus</i>	125
63.	<i>Carcharhinus galapagensis</i> , proportional dimensions in percentage of total length	129
64.	Vertebral numbers in 15 specimens of <i>Carcharhinus galapagensis</i>	130
65.	Length of first dorsal fin base as percentage of total length in <i>Carcharhinus brachyurus</i> and <i>C. plumbeus</i>	137
66.	<i>Carcharhinus plumbeus</i> , proportional dimensions in percentage of total length	139
67.	Vertebral numbers in seven specimens of <i>Carcharhinus plumbeus</i>	140
68.	Precaudal vertebral numbers in <i>Carcharhinus plumbeus</i>	140
69.	Number of embryos per litter, size at birth, size of mature specimens, and maximum size of <i>Carcharhinus plumbeus</i>	140
70.	<i>Carcharhinus altimus</i> , proportional dimensions in percentage of total length	144
71.	<i>Carcharhinus perezii</i> , proportional dimensions in percentage of total length	149
72.	Vertebral numbers in two specimens of <i>Carcharhinus perezii</i>	150
73.	<i>Carcharhinus longimanus</i> , proportional dimensions in percentage of total length	156
74.	Vertebral numbers in seven specimens of <i>Carcharhinus longimanus</i>	157
75.	<i>Carcharhinus falciformis</i> , proportional dimensions in percentage of total length	161
76.	Vertebral numbers in 19 specimens of <i>Carcharhinus falciformis</i>	163
77.	Frequency distribution of precaudal vertebral numbers in <i>Carcharhinus falciformis</i>	163
78.	Clasper length as percentage of total length in <i>Carcharhinus falciformis</i>	163
79.	Number of embryos per litter, size at birth, size at maturity, and maximum size in <i>Carcharhinus falciformis</i>	163
80.	<i>Carcharhinus sorrah</i> , proportional dimensions in percentage of total length	169
81.	Vertebral numbers in 14 specimens of <i>Carcharhinus sorrah</i>	170
82.	Number of embryos per litter and size of embryos in <i>Carcharhinus sorrah</i>	170
83.	<i>Carcharhinus brachyurus</i> , proportional dimensions in percentage of total length	176

24.	Frequency distribution of number of monospondylous centra in <i>Carcharhinus dussumieri</i> and <i>C. sealei</i>	58
25.	Vertebral numbers and proportional dimensions used in referring various nominal species to either <i>Carcharhinus dussumieri</i> or <i>C. sealei</i>	58-59
26.	<i>Carcharhinus dussumieri</i> , proportional dimensions in percentage of total length	61
27.	Vertebral numbers in 33 specimens of <i>Carcharhinus dussumieri</i>	63
28.	Clasper length as percentage of total length in <i>Carcharhinus dussumieri</i>	63
29.	Proportional dimensions showing that the holotype of <i>Carcharhinus remotus</i> agrees more closely with specimens of <i>C. acronotus</i> than with specimens of <i>C. remotus</i> sensu Bigelow & Schroeder	68
30.	<i>Carcharhinus acronotus</i> , proportional dimensions in percentage of total length	68
31.	Vertebral numbers in four specimens of <i>Carcharhinus acronotus</i>	69
32.	Proportional dimensions showing differences between Asian and American specimens of <i>Carcharhinus porosus</i>	72
33-34.	<i>Carcharhinus porosus</i> , proportional dimensions in percentage of total length	73-74
35.	Vertebral numbers in 35 specimens of <i>Carcharhinus porosus</i>	75
36.	Frequency distribution of precaudal and caudal vertebral numbers in <i>Carcharhinus porosus</i>	76
37.	Proportional dimensions of penultimate monospondylous centrum and first diplospondylous centrum in 31 specimens of <i>Carcharhinus porosus</i>	76
38.	<i>Carcharhinus fitzroyensis</i> , proportional dimensions in percentage of total length	80
39.	Precaudal vertebral numbers, proportional dimensions, and dental formulae used in referring various nominal species to either <i>Carcharhinus amboinensis</i> or <i>C. leucas</i>	84-85
40.	<i>Carcharhinus leucas</i> , proportional dimensions in percentage of total length	87
41.	Vertebral numbers in 53 specimens of <i>Carcharhinus leucas</i>	89
42.	Precaudal vertebral numbers in <i>Carcharhinus leucas</i> from different localities	89
43.	Clasper length as percentage of total length in <i>Carcharhinus leucas</i>	89
44.	Size of pregnant females, number of embryos per litter, and size of embryos in <i>Carcharhinus leucas</i>	90
45.	Frequency distribution of number of teeth on each side of lower jaw in <i>Carcharhinus amboinensis</i> and <i>C. leucas</i>	93
46.	<i>Carcharhinus amboinensis</i> , proportional dimensions in percentage of total length	95
47.	Vertebral numbers in 18 specimens of <i>Carcharhinus amboinensis</i>	95
48.	<i>Carcharhinus melanopterus</i> , proportional dimensions in percentage of total length	99
49.	Vertebral numbers in 26 specimens of <i>Carcharhinus melanopterus</i>	100
50.	<i>Carcharhinus cautus</i> , proportional dimensions in percentage of total length	105
51.	Vertebral numbers in four specimens of <i>Carcharhinus cautus</i>	106
52.	<i>Carcharhinus amblyrhynchos</i> , proportional dimensions in percentage of total length	109
53.	Vertebral numbers in three specimens of <i>Carcharhinus amblyrhynchos</i>	110
54.	Proportional dimensions indicating differences between <i>Carcharhinus wheeleri</i> and <i>C. amblyrhynchos</i>	113
55.	<i>Carcharhinus wheeleri</i> n. sp., proportional dimensions in percentage of total length	115
56.	Vertebral numbers in two specimens of <i>Carcharhinus wheeleri</i>	115
57.	Number of embryos per litter, size at birth, size at maturity, and maximum size of <i>Carcharhinus wheeleri</i>	116
58.	<i>Carcharhinus albimarginatus</i> , proportional dimensions in percentage of total length	119
59.	Vertebral numbers in two specimens of <i>Carcharhinus albimarginatus</i>	120
60.	Proportional dimensions showing differences between <i>Carcharhinus obscurus</i> and <i>C. galapagensis</i>	122
61.	<i>Carcharhinus obscurus</i> , proportional dimensions in percentage of total length	123
62.	Vertebral numbers in 10 specimens of <i>Carcharhinus obscurus</i>	125
63.	<i>Carcharhinus galapagensis</i> , proportional dimensions in percentage of total length	129
64.	Vertebral numbers in 15 specimens of <i>Carcharhinus galapagensis</i>	130
65.	Length of first dorsal fin base as percentage of total length in <i>Carcharhinus brachyurus</i> and <i>C. plumbeus</i>	137
66.	<i>Carcharhinus plumbeus</i> , proportional dimensions in percentage of total length	139
67.	Vertebral numbers in seven specimens of <i>Carcharhinus plumbeus</i>	140
68.	Precaudal vertebral numbers in <i>Carcharhinus plumbeus</i>	140
69.	Number of embryos per litter, size at birth, size of mature specimens, and maximum size of <i>Carcharhinus plumbeus</i>	140
70.	<i>Carcharhinus altimus</i> , proportional dimensions in percentage of total length	144
71.	<i>Carcharhinus perezii</i> , proportional dimensions in percentage of total length	149
72.	Vertebral numbers in two specimens of <i>Carcharhinus perezii</i>	150
73.	<i>Carcharhinus longimanus</i> , proportional dimensions in percentage of total length	156
74.	Vertebral numbers in seven specimens of <i>Carcharhinus longimanus</i>	157
75.	<i>Carcharhinus falciformis</i> , proportional dimensions in percentage of total length	161
76.	Vertebral numbers in 19 specimens of <i>Carcharhinus falciformis</i>	163
77.	Frequency distribution of precaudal vertebral numbers in <i>Carcharhinus falciformis</i>	163
78.	Clasper length as percentage of total length in <i>Carcharhinus falciformis</i>	163
79.	Number of embryos per litter, size at birth, size at maturity, and maximum size in <i>Carcharhinus falciformis</i>	163
80.	<i>Carcharhinus sorrah</i> , proportional dimensions in percentage of total length	169
81.	Vertebral numbers in 14 specimens of <i>Carcharhinus sorrah</i>	170
82.	Number of embryos per litter and size of embryos in <i>Carcharhinus sorrah</i>	170
83.	<i>Carcharhinus brachyurus</i> , proportional dimensions in percentage of total length	176

84.	Vertebral numbers in 28 specimens of <i>Carcharhinus brachyurus</i>	177
85.	<i>Carcharhinus borneensis</i> , proportional dimensions in percentage of total length	181
86.	Vertebral numbers in the holotype of <i>Carcharias (Prionodon) borneensis</i>	182
87.	<i>Carcharhinus</i> species in the four principal tropical shore fish regions	182
88.	<i>Carcharhinus</i> species of the Indo-Pacific region	183
89.	<i>Carcharhinus</i> species of the eastern Indian-western Pacific subregions and of Australia	184
90.	<i>Carcharhinus</i> species of the eastern Atlantic, Mediterranean, and Red Sea	184
91.	Distribution of <i>Carcharhinus</i> species-pairs	185



Sharks of the Genus *Carcharhinus*

J. A. F. GARRICK¹

ABSTRACT

The genus *Carcharhinus* Blainville contains 25 living species of whaler sharks, one of which (*C. wheeleri*) is described as new while the other 24 incorporate 95 identifiable nominal species which fall into the limits of the genus as here recognized. Features studied include morphometrics, external morphology, color, tooth numbers and shapes, vertebral numbers and other vertebral characteristics, and biological data. The systematic value of these features is reviewed, and it is concluded that despite their importance at the specific level they do not in general allow firm statements on subgeneric groupings or on the relationship between *Carcharhinus* and other similar genera. Accordingly, no formal subdivision of the genus is proposed, and the limits and characterization of the genus are essentially as in Bigelow and Schroeder (1948) except that the following six nominal species are excluded because of one or more notably divergent aspects of their morphology: *Carcharias gangeticus* Müller and Henle, *C. glyphis* M. and H., *C. oxyrhynchus* M. and H., *C. temminckii* M. and H., *Carcharhinus tephrodes* Fowler, and *Carcharhinus velox* Gilbert. A further 13 nominal species are treated as species dubia.

Long-established names for two species, *Carcharhinus limbatus* Valenciennes and *C. sorrah* Val., are retained though each has a poorly founded senior synonym; their cases must be put to the International Commission of Zoological Nomenclature. A neotype is designated for *brachyurus* Günther, and lectotypes are designated for *dussumieri* Val., *henlei* Val., *malabaricus* Day, *menisorrh* Val., *pleurotaenia* Bleeker, *sorrah* Val., and *tjutjot* Bleeker.

A key is given to differentiate the species. For each species primary synonyms are listed and discussed and a diagnosis and description are given. Descriptions include measurements and counts and line illustrations that show the whole shark in lateral view, underside of head, nostril, and teeth. The geographic distribution is described, and biological data on number of embryos, size at birth, size at sexual maturity, and maximum size are summarized.

The 25 species are predominantly tropical-subtropical, but only two appear to be confined to the tropics and seven have been recorded from the tropics to latitudes as high as 40°. Most are coastal, one is virtually insular, and one, or perhaps two, enter fresh or brackish water. Eight species are worldwide; 23 occur in the Indo-Pacific, 13 in the western Atlantic, 11 in the eastern Atlantic, 10 in the eastern Pacific, and 5 in the Mediterranean.

INTRODUCTION

The prime purpose of this account is an alpha taxonomy of the genus *Carcharhinus*. This genus, worldwide in distribution, contains the whaler sharks, many of which grow to a rather large size (up to 3.6 m long) and hence are conspicuous elements of the marine fauna, particularly in tropical-subtropical regions although some of them extend also into temperate latitudes. Most are coastal or shelf dwelling but a few are regular inhabitants of the open ocean and at least one occurs in freshwater rivers or lakes with access to the sea.

A few of the species are easily recognized and well known, principally because they have characteristic color patterns of dark or white fin tips, but many of the others are superficially very similar and readily confused. For this reason they are, in general, poorly known and not readily identified in most parts of the world. Also, the slow rate at which knowledge has accumulated on those features which are important in diagnosing the species has meant that many species have been described several times under different names—on average 3.8 times (range 1-10) for all of the species according to my findings. A revision of *Carcharhinus* on a worldwide basis is, therefore, long overdue. No comprehensive treatment of the genus has appeared since the last century, when Müller and Henle (1841) and Dumeril (1865) dealt with the species known to them at that time; many species have been proposed since then. Regional accounts or revisions over the last three decades have alleviated

the situation, with varying success in resolving problems with the species in the areas dealt with. Amongst such accounts should be mentioned those of Bigelow and Schroeder (1948) and Springer (1950) for the western North Atlantic, Tortonese (1950, 1951b) for the Mediterranean, Rosenblatt and Baldwin (1958) for the eastern Pacific, Fourmanoir (1961) for Madagascar, Gohar and Mazhar (1964) for the Red Sea, and Bass et al. (1973) for the western Indian Ocean (this last mentioned revision being the most definitive, comprehensive, and broadly applicable of them all). However, all of these have suffered to a greater or lesser degree in having insufficient comparative material for study, and, in particular, access to the surprisingly extensive range of type material still existing and which must be studied if the status of many of the nominal species is to be established with confidence. In the present study I have been fortunate in being able to examine type material of 62 of the 95 nominal species which contribute to the synonymy of the 25 species I recognize as valid. No type material, other than a possible syntype of *falcipinnis* Lowe, 1839, was found for the further 13 species treated here as species dubia.

Features used in this study for the identification and diagnosis of the species are for the most part those that have been traditionally applied, including morphometrics, size, various aspects of external morphology such as, for example, snout and fin shapes or the presence or absence of a middorsal dermal ridge, tooth numbers and shapes, and color. Supplementing these features, and providing virtually indispensable information for separating some species, are data on the vertebrae, particularly vertebral numbers, relative lengths and diameters of some vertebrae, and the position at which diplospondyly occurs. Although these features in total allow the species to be

¹Department of Zoology, Victoria University of Wellington, Private Bag, Wellington, New Zealand.

distinguished, they do not appear to provide, either individually or in combination, a ready means of establishing subgeneric relationships; correlation between the features is at a low level. A few species pairs can be recognized, in which the members of each pair share so closely the same features that they can be regarded as siblings, and in a few other cases a group of three or more species share a rather more diffuse combination of common characteristics, but overall there is no obvious pattern of subgeneric groupings. This heterogeneity is further compounded by other species which share or approximate closely to many of the characteristics of other carcharhinid genera, notably *Rhizoprionodon*, *Aprionodon*, and *Hypoprion*. My data do not allow me to resolve with confidence the relationship between *Carcharhinus* and these other genera. Accordingly I believe that the best course to follow at this stage is, firstly to retain essentially the status quo in terms of the limits or definition of the genus *Carcharhinus*, and secondly not to formally subdivide the genus but instead simply to indicate the possible species groupings within it. It follows that the main contribution which this study can make is in species identification, together with collated information on distribution and some aspects of the biology of the species, and in resolving primary synonymic and nomenclatural problems which have long beset previous studies of the genus.

On the above basis *Carcharhinus* is defined for the purposes of this study on virtually the same features used by previous workers and exemplified by the definitions in Bigelow and Schroeder (1948) and Bass et al. (1973).

However, my definition of the genus differs in some respects, the purpose of this being to exclude a few species that seem sufficiently distinct to warrant generic separation from *Carcharhinus*. The most divergent of these species is *Carcharias* (*Prionodon*) *oxyrhynchus* Müller and Henle, 1841 (type species of *Isogomphodon* Gill, 1862) in which the high number of teeth (more than 50 in row around upper or lower jaw), the broad paddle-shaped pectorals, and the long narrow pointed snout are obvious features, amongst others, that make it quite unlike any species of *Carcharhinus*. Four other nominal species [*Carcharias* (*Prionodon*) *temminckii* Müller and Henle, 1841 (type species of *Lamiopsis* Gill, 1862), *Carcharhinus* *tephrodes* Fowler, 1905 (which appears synonymous with *temminckii*), *Carcharias* (*Prionodon*) *gangeticus* Müller and Henle, 1841 and *C. (P.) glyphis* Müller and Henle, 1841 (type species of *Glyphis* Agassiz, 1843 by absolute tautonymy according to Compagno²)] are excluded because they have an upper precaudal pit which is ovoid, longer than wide, with poorly marked edges or borders, and thus markedly different from that of *Carcharhinus* species which is crescent-shaped, wider than long, with a well-marked anterior edge or border. These four species excluded on this feature vary in the extent to which they otherwise resemble species of *Carcharhinus* in morphometrics, external morphology, and teeth, and it is unlikely that they constitute a natural group. The last-mentioned two (*gangeticus* and *glyphis*) share many similarities with each other and differ less from *Carcharhinus* than does *temminckii*.

Treatment of *oxyrhynchus* and *temminckii* comparable to that above is evident from Compagno's (1973a) outline classification of the Carcharhininae in which *Isogomphodon* and *Lamiopsis* are listed amongst the genera. However, Compagno does not include *Aprionodon* in his list of genera,

whereas the definition of *Carcharhinus* that I am using separates *Aprionodon* from *Carcharhinus* because of the smooth-edged teeth of the former. The validity of excluding *Aprionodon* from *Carcharhinus* on this dental character alone is admittedly subjective, but is adopted here for convenience pending information on other characteristics which will better establish the relationships between these genera. Lastly, one other species that I exclude from *Carcharhinus* is *Carcharhinus velox* Gilbert in Jordan and Evermann, 1898 which differs strikingly from all of the other species in its long snout and large, transverse nostril openings set so closely together that the internarial distance is only slightly greater than the nostril width. Also, according to Compagno,³ *velox* has cranial features unlike any other *Carcharhinus* species he has studied.

MATERIALS

Materials used in this study came from a wide variety of sources but principally were preserved specimens in the collections of museums and other institutions listed below. In a few cases fresh specimens were made available for me, chiefly in North America, Hawaii, and South Africa. Many colleagues also generously supplied radiographs of specimens and data that I was able to incorporate even though I did not see the specimens.

The following abbreviations have been used in the text:

AMNH	American Museum of Natural History, New York
AMS	Australian Museum, Sydney
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	British Museum (Natural History), London
CNHM	Chicago Natural History Museum (now Field Museum of Natural History)
CU	Cornell University, Ithaca
DIRU	Department of ichthyology (now J.L.B. Smith Institute of Ichthyology), Rhodes University, Grahamstown, South Africa
DM	Dominion Museum (now National Museum) Wellington, New Zealand
FSBC	Florida State Board of Conservation (now Florida Department of Natural Resources), St. Petersburg
GVF	George Vanderbilt Foundation, Stanford, Calif., specimens now at California Academy of Sciences
HU	Hebrew University of Jerusalem, Israel
IFAN	Institut Français d'Afrique Noire, Dakar, Senegal
IRSN	Institut Royal des Sciences Naturelles de Belgique, Brussels
ISH	Institut für Seefischerei, Hamburg
ISZZ	Institut für Spezielle Zoologie und Zoologisches Museum, Berlin
MCZ	Museum of Comparative Zoology, Harvard University
MNHN	Museum National d'Histoire Naturelle, Paris
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium
MSNG	Museo Civico di Storia Naturale, Genoa
NMV	Naturhistorisches Museum, Vienna
NZOI	New Zealand Oceanographic Institute, Wellington
ORID	Oceanographic Research Institute, Durban

²L. J. V. Compagno, Division of Systematic Biology, Stanford University, Stanford, CA 94305, pers. commun. April 1974.

³L. J. V. Compagno, Division of Systematic Biology, Stanford University, Stanford, CA 94305, pers. commun. March 1971.

QMB	Queensland Museum, Brisbane
RNH	Rijksmuseum van Natuurlijke Historie, Leiden
SAMC	South African Museum, Capetown
SFRH	Sea Fisheries Research Station, Haifa
SIO	Scripps Institution of Oceanography, La Jolla
SMF	Natur-Museum und Forschungs-Institut, Senckenberg, Frankfurt
SMNS	Staatliches Museum für Naturkunde, Stuttgart
SOSC	Smithsonian Oceanographic Sorting Center, Washington, D.C.
SU	Division of Systematic Biology, Stanford University; specimens now at California Academy of Sciences, San Francisco
UCLA	University of California, Los Angeles
UMML	University of Miami Institute of Marine Science, Miami
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
UPR	University of Puerto Rico, Mayaguez
USNM	United States National Museum, Washington, D.C.
UZMK	Universitetets Zoologiske Museum, Copenhagen
WAM	Western Australian Museum, Perth
ZSZM	Zoologisches Staatinstitut und Zoologisches Museum, Hamburg

METHODS

Measurements

The measurements used to calculate the proportional dimensions given here were made as exemplified in Figure 1. Longitudinal measurements, e.g., total length (TL) and distances from snout tip to various points along the body, were taken between vertical projections to the horizontal axis of the body, and hence are not diagonal (i.e., point to point) nor measured round the curve of the body. The methods for making these and other measurements were essentially as described in detail by Springer (1964) except for the following:

Snout tip to mouth: measured to the posterior edge of the upper lip at the ventral midline.

Snout to gill openings: measured to the most anterior part of each gill opening.

Mouth length: distance from the posterior edge of the upper lip at the ventral midline to the midpoint of a line connecting the two corners of the mouth.

Counts

Teeth.—The dental formulae for each species give the number of teeth around the outer margin of the upper jaw (above line) and the lower jaw (below line). Each upper and lower jaw count is subdivided into the number of teeth on the left side, followed by the number of noticeably small, central, or symphyseal teeth (if any), then the number of teeth on the right side. The teeth counted around the margin of each jaw in this way constitute a row. Each tooth of the row is the outer element of a file or series of teeth aligned inwards and derived from the same tooth primordium. Thus each series is made up of one or more functional teeth together with their developing replacements.

Vertebrae.—Most of the vertebral counts presented here were

made from radiographs, using fine-grain industrial X-ray film. In a few cases, where large, fresh sharks were examined and could not be preserved, counts were made by dissection. The total count for each specimen was subdivided into:

Precaudal count: all complete centra anterior to the forward edge of the upper precaudal pit.

Caudal count: all centra posterior to the precaudal centra.

In order to ensure that the separation point between precaudal and caudal centra was clearly identifiable from the radiograph, a pin was inserted into the vertebral column dorsally at the anterior edge of the upper precaudal pit before each specimen was X-rayed.

Vertebral counts published by other authors and included in the present study are not necessarily entirely comparable to mine, although as far as could be ascertained the differences are relatively minor. For example, the numerous precaudal counts from Bass et al. (1973) include all complete centra anterior to the center of the upper precaudal pit. Examination of my radiographs suggests that this more posterior separation point involves an extra distance not exceeding the length of one centrum and in most cases much less than that. On average the extra distance is likely to be about one-half of a centrum length.

The position at which the precaudal vertebrae change from being monospondylous to diplospondylous was noted from the radiographs, on the assumption that this transition is evidenced by an abrupt reduction in centrum length at or near the pelvic region. In many species the transition from long monospondylous centra to short diplospondylous centra was very obvious, but in others it was less evident and could only be confirmed by measuring the lengths of the centra. For most species diplospondyly begins above the pelvic fin, but exceptionally it is just anterior to the pelvic fin origin or as far posterior as the second dorsal fin.

In some species the diplospondylous centra alternate slightly but regularly in length. In a few the lengths are much more irregular, with long (seemingly monospondylous) centra interspersed amongst the short centra. However, even in these last-mentioned examples the position of the first short centrum was taken as the transition to diplospondyly.

More detailed descriptions of the methods and problems in making vertebral counts in sharks are given in Springer (1964) and Springer and Garrick (1964).

CONSIDERATION OF SOME CHARACTERS USED IN STUDY

Morphometrics.—Insofar as many of the nominal species were originally described as distinct on the basis of differences in proportional dimensions, it is appropriate to present a broad range of data on the latter for the genus as a whole so that the usefulness of proportions can be evaluated. The data so presented (Figs. 2-8) are, with very few exceptions, from measurements made in this study. They include, firstly, a series of presentations (Figs. 2-5) in which the proportions of various features are expressed as percentages of total length, and secondly, a series (Figs. 6-8) in which direct comparison is made between various of these features. The features selected for presentation cover only some of those examined in the study, and were chosen on one or more of three grounds: either they are features which have commonly been used in the past, or they

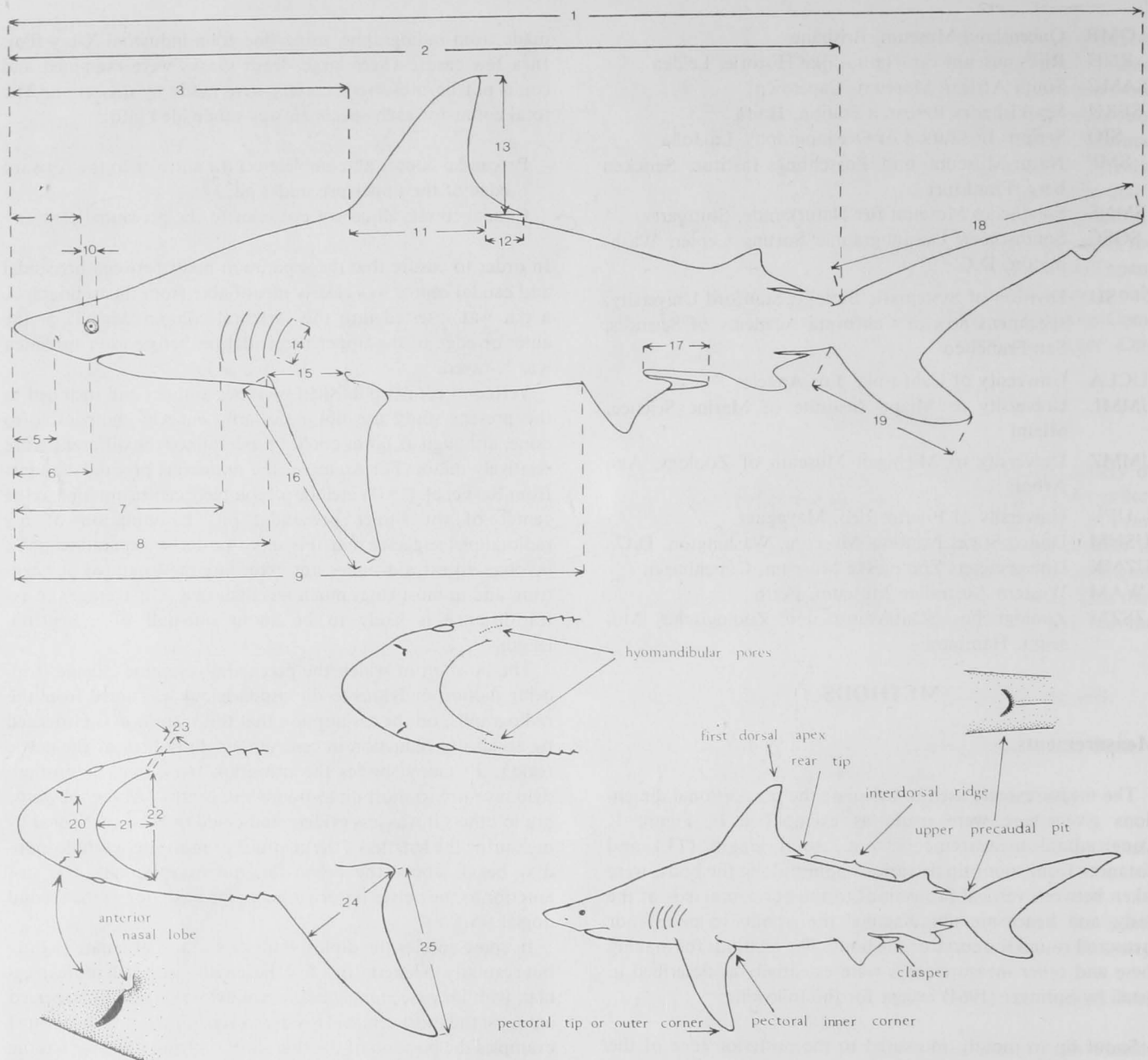


Figure 1.—Examples of measurements made in this study and some terminology of structures: 1, total length; 2, snout tip to upper caudal origin; 3, snout tip to first dorsal origin; 4, snout tip to eye; 5, snout tip to outer nostrils (prenarial length); 6, snout tip to mouth (preoral length); 7, snout tip to first gill opening; 8, snout tip to pectoral origin; 9, snout tip to pelvic origin; 10, horizontal diameter of eye; 11, length of base of first dorsal; 12, length of posterior margin or rear tip of first dorsal; 13, vertical height of first dorsal; 14, length of fifth gill opening; 15, length of pectoral base; 16, length of anterior margin of pectoral; 17, length of clasper; 18, length of dorsal or upper lobe of caudal; 19, length of ventral or lower lobe of caudal; 20, distance between inner corners of nostrils (internarial distance); 21, length of mouth; 22, width of mouth; 23, length of upper labial furrow; 24, greatest width of pectoral; 25, length of distal margin of pectoral.

have been found to have value in the present study, or they contribute to a broad picture of morphometrics in the genus and in so doing do not necessarily assist in distinguishing between species (or conversely in indicating relationships between species).

Perusal of these data shows that for most features there is a wide range of variation within each species, and very marked overlap between species. The effect of this is that many proportions have virtually no predictive value for identifying species, and even the best of them, i.e., those in which there is least overlap between species, still have a low level of usefulness when considered alone. Because data for many of the species are far from adequate it is likely that more information would reduce even further the apparent usefulness of these proportions.

The above commentary does not mean that proportional dimensions no longer have a significant place in species recognition in *Carcharhinus*. The use of proportions in conjunction with other characters which delimit the number of species to be considered greatly enhances the value of the former. Also, if consideration is given to allometric growth and the consequent changes in proportions (the several patterns of which were documented and discussed in Bass 1973) the usefulness of proportions is further extended. In some cases, and notably for those nominal species for which there is no type material, proportional dimensions as given in the original description or shown by illustrations provide the major or prime evidence for identification.

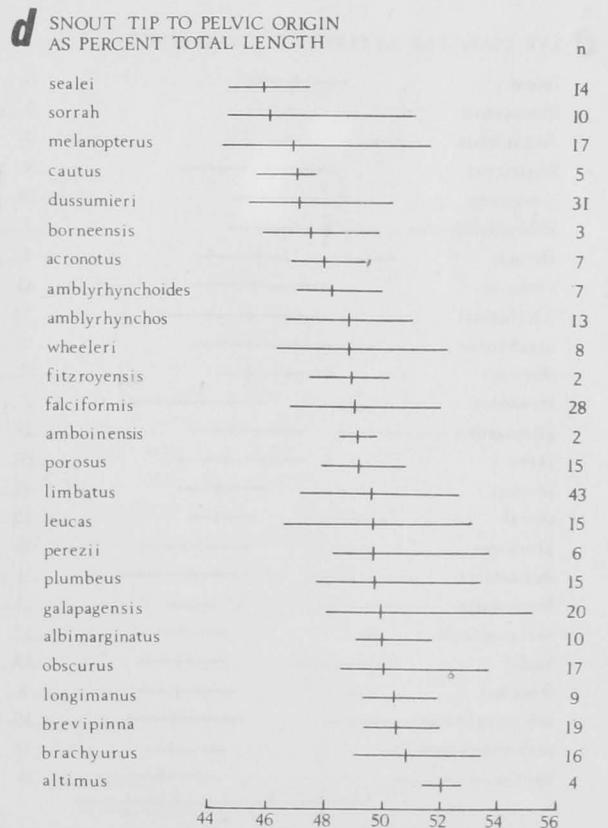
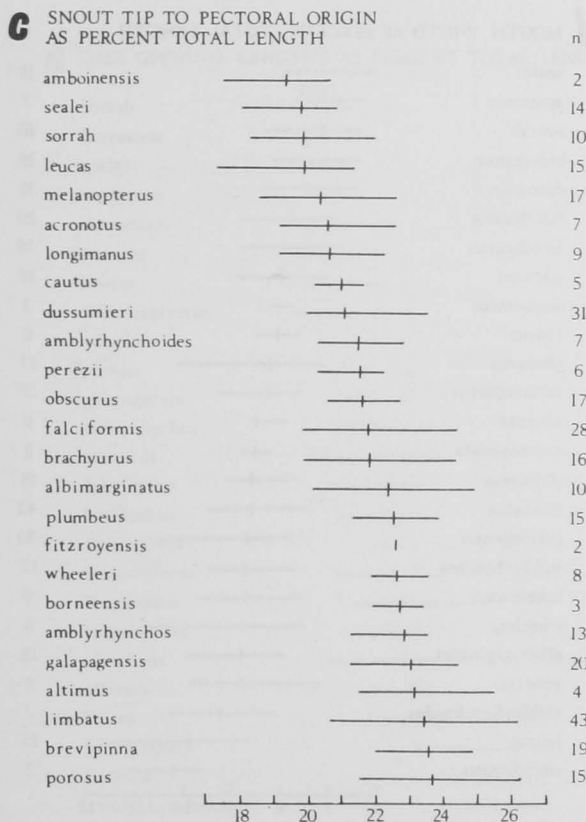
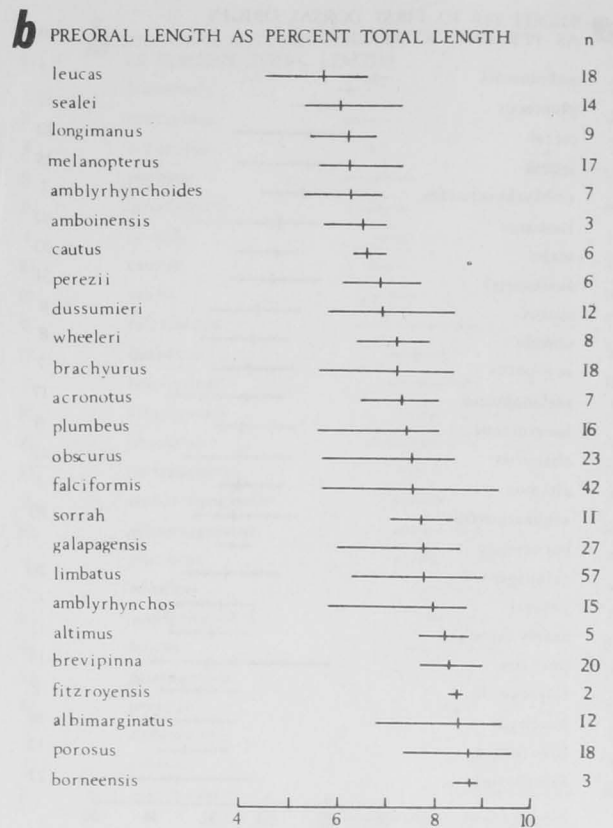
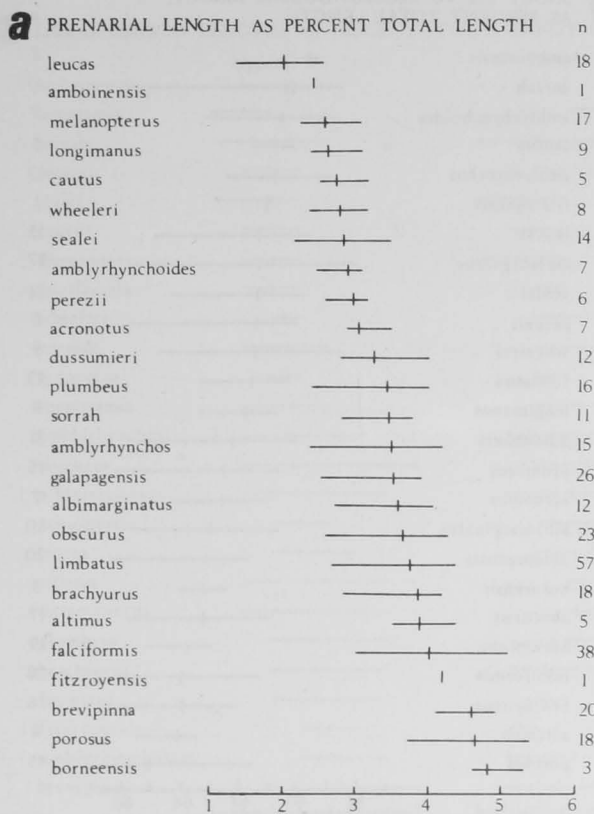


Figure 2.—Proportional dimensions of 25 species of *Carcharhinus*: a, prenarial length as percent of total length; b, preoral length as percent of total length; c, snout tip to pectoral origin as percent of total length; d, snout tip to pelvic origin as percent of total length (horizontal lines represent ranges; vertical lines are means; n = number of specimens).

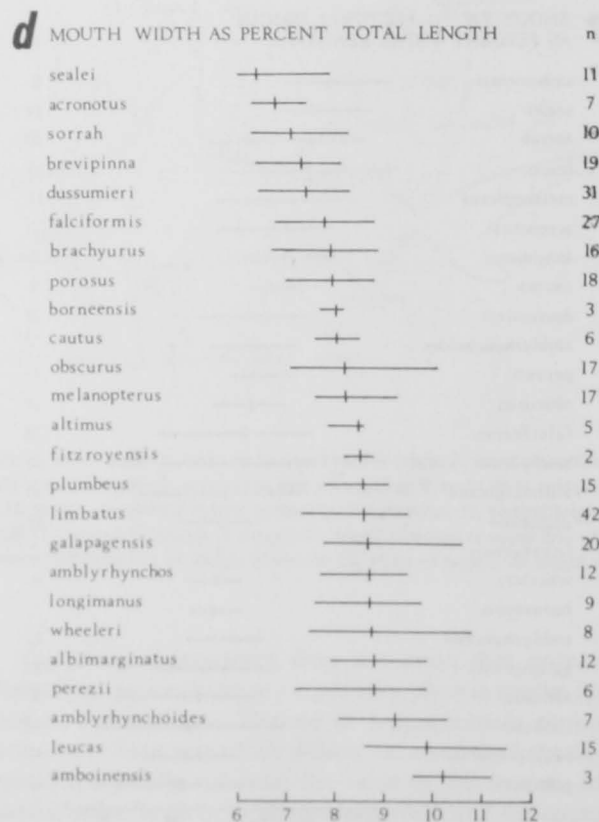
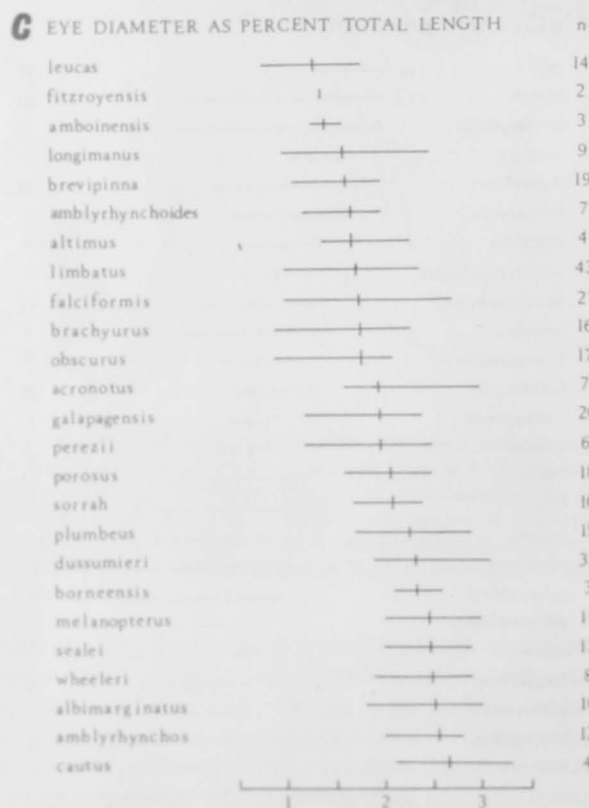
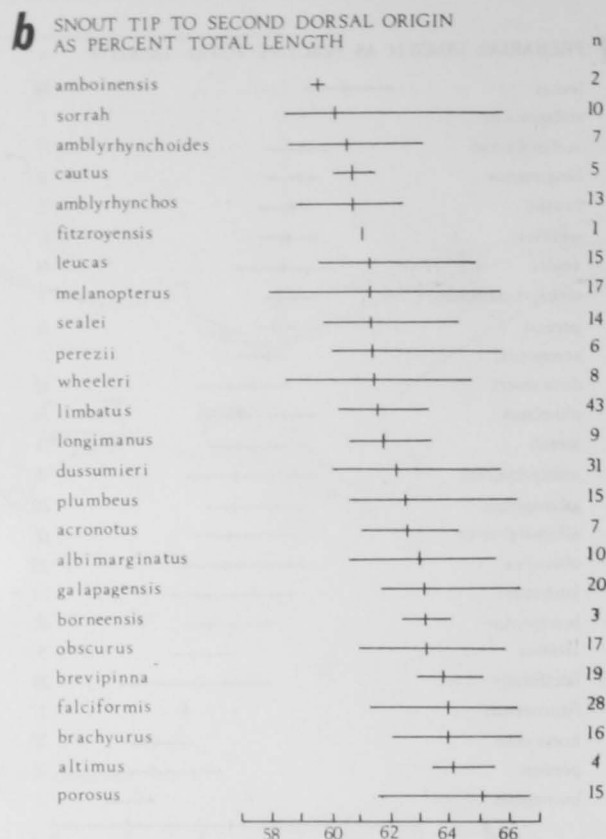
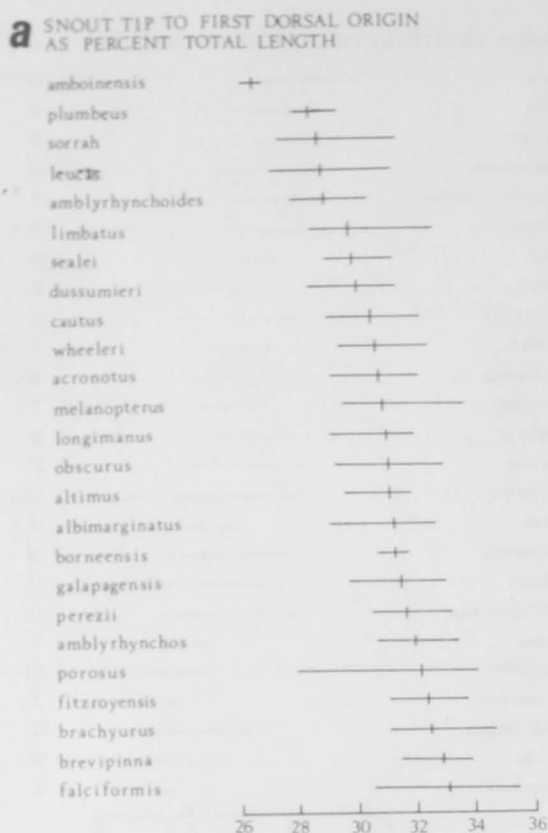


Figure 3.—Proportional dimensions of 25 species of *Carcharhinus*: a, snout tip to first dorsal fin origin as percent of total length; b, snout tip to second dorsal fin origin as percent of total length; c, horizontal diameter of eye as percent of total length; d, mouth width as percent of total length (horizontal lines represent ranges; vertical lines are mean; n = number of specimens).

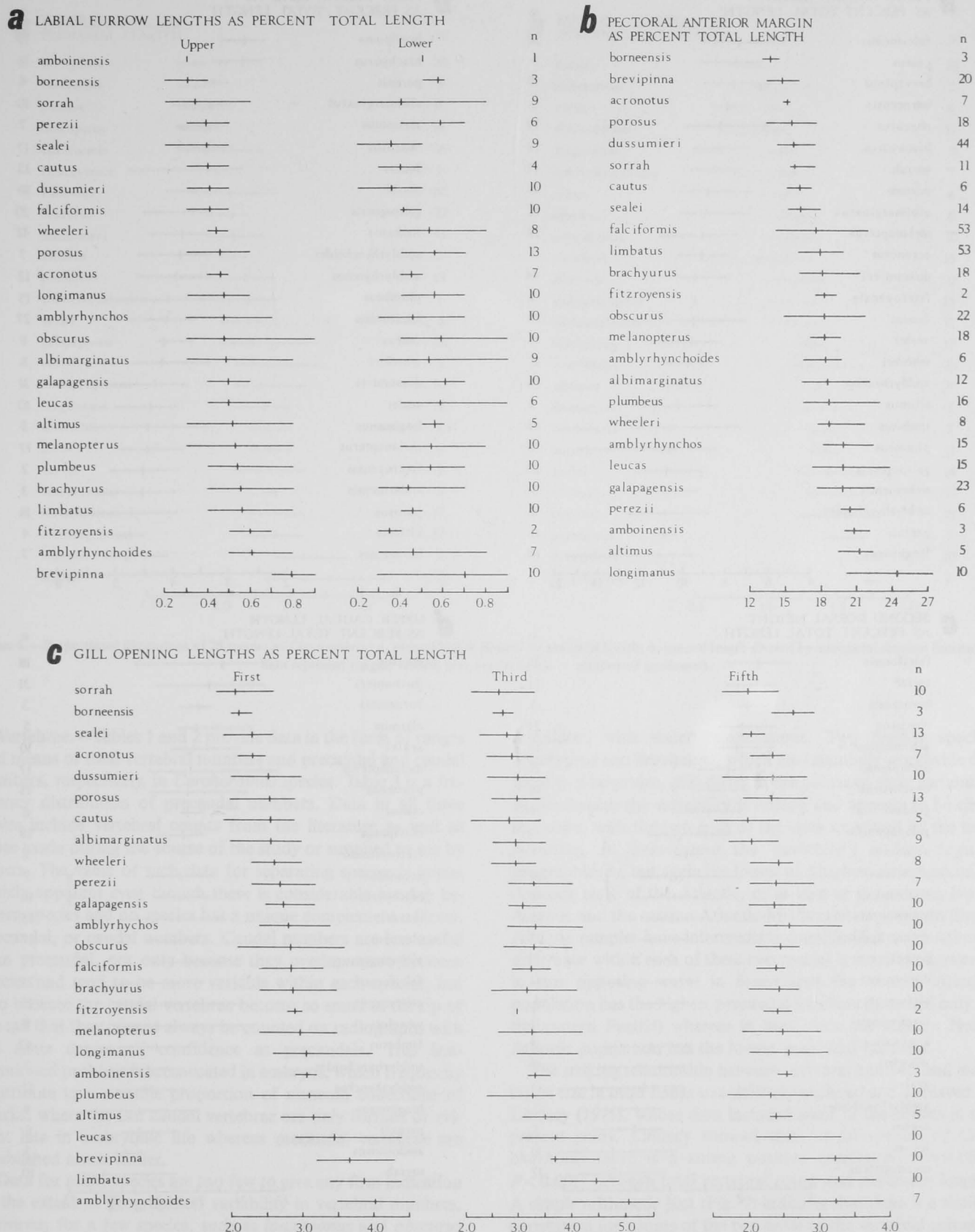


Figure 4.—Proportional dimensions of 25 species of *Carcharhinus*: a, upper and lower labial furrow lengths as percent of total length; b, pectoral fin anterior margin as percent of total length; c, first, third, and fifth gill opening lengths as percent of total length (horizontal lines represent ranges; vertical lines are means; n = number of specimens).

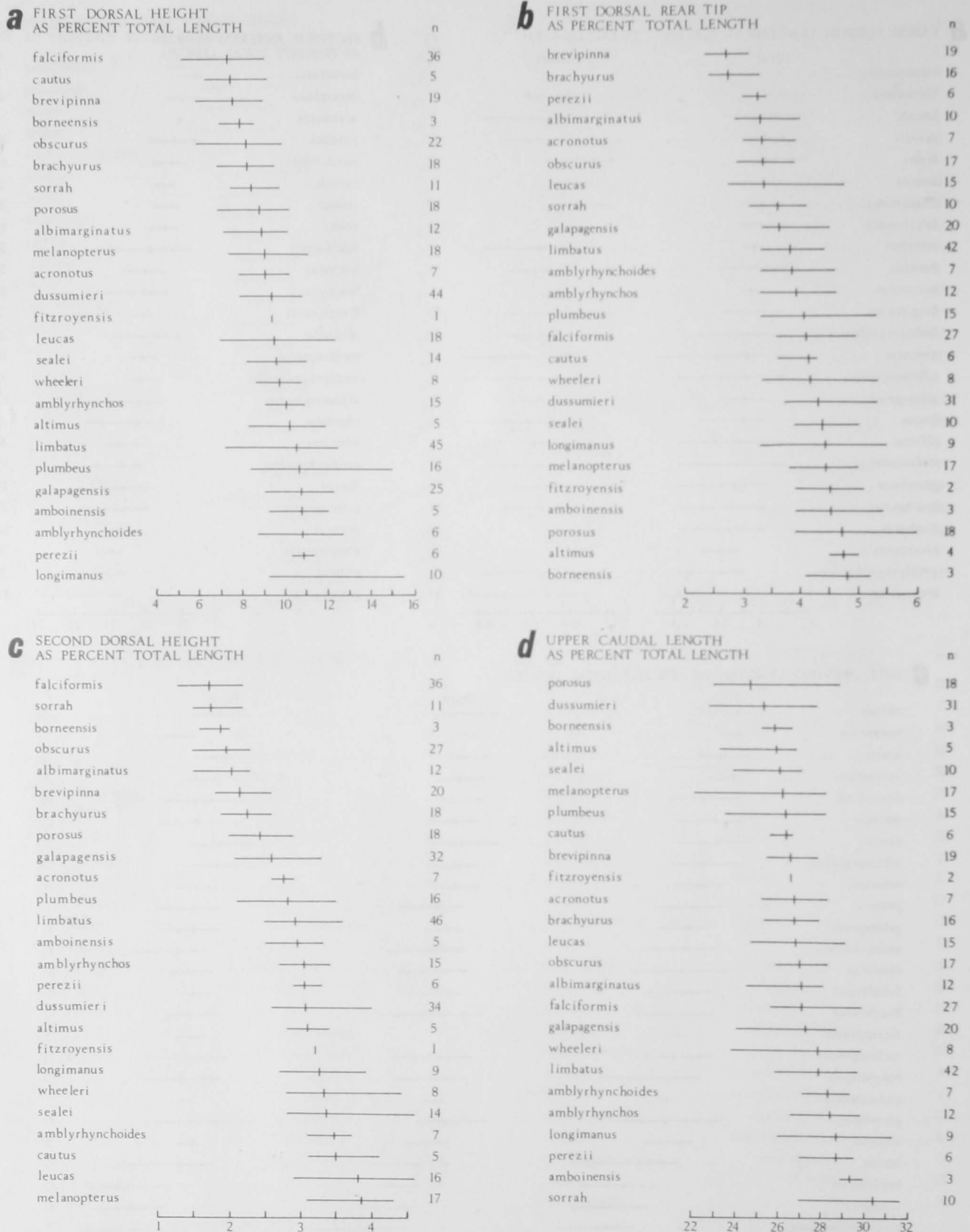


Figure 5.—Proportional dimensions of 25 species of *Carcharhinus*: a, first dorsal fin height as percent of total length; b, first dorsal fin rear tip as percent of total length; c, second dorsal fin height as percent of total length; d, upper caudal lobe length as percent of total length (horizontal lines represent ranges; vertical lines are means; n = number of specimens).

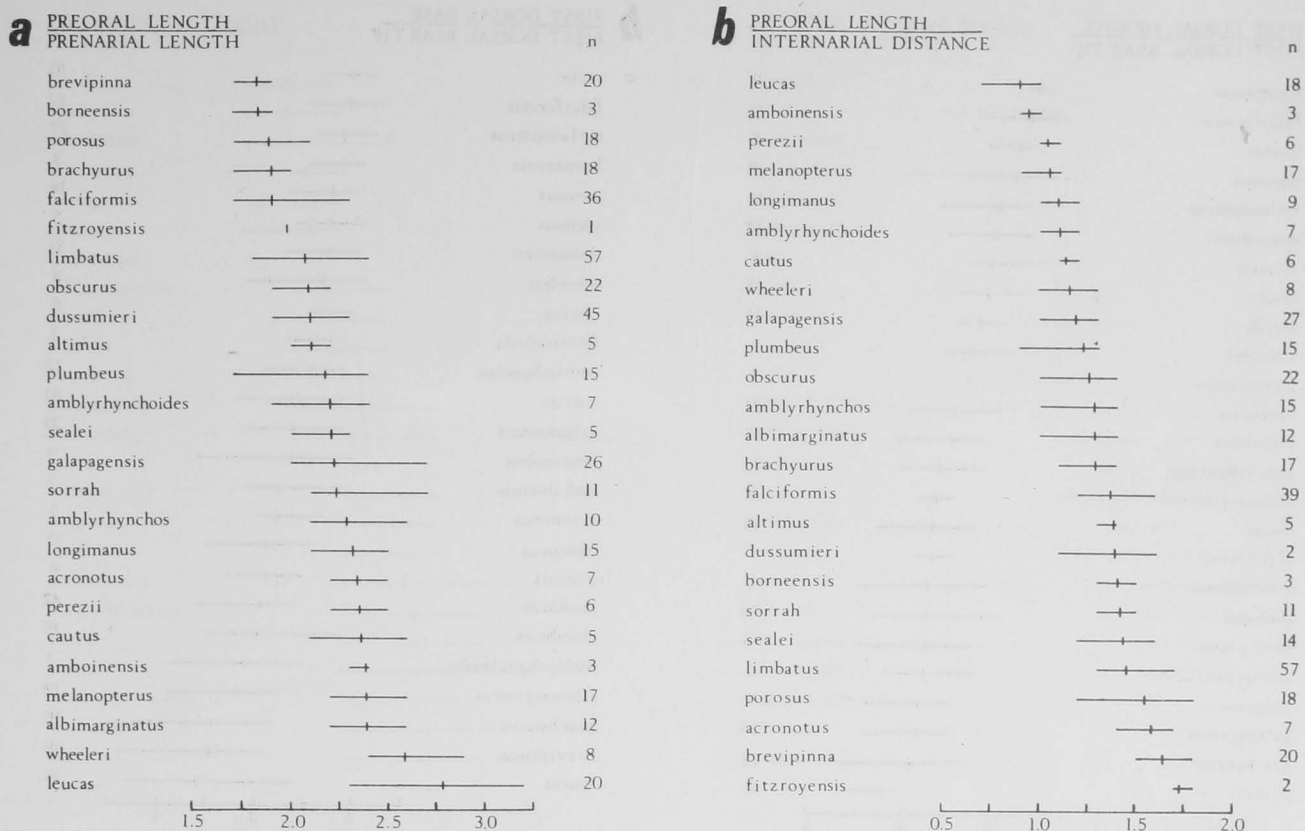


Figure 6.—Proportional dimensions of 25 species of *Carcharhinus*: a, preoral length divided by prenarial length; b, preoral length divided by internarial distance (horizontal lines represent ranges; vertical lines are means; n = number of specimens).

Vertebrae.—Tables 1 and 2 provide data in the form of ranges and means of total vertebral numbers and precaudal and caudal numbers, respectively, in *Carcharhinus* species. Table 3 is a frequency distribution of precaudal numbers. Data in all three tables include vertebral counts from the literature as well as those made during the course of the study or supplied to me by others. The value of such data for separating species is immediately apparent even though there is considerable overlap between species and no species has a unique complement of total, precaudal, or caudal numbers. Caudal numbers are less useful than precaudal, not only because they overlap more between species and tend to be more variable within each species, but also because the caudal vertebrae become so small at the tip of the tail that they cannot always be counted on radiographs with the same degree of confidence as precaudals. This last-mentioned problem is accentuated in embryos, which frequently contribute to a sizeable proportion of museum collections of sharks, where the last caudal vertebrae are only formed or evident late in embryonic life whereas precaudal vertebrae are established much earlier.

Data for many species are too few to give any firm indication of the extent of geographical variability in vertebral numbers. However, for a few species, such as *longimanus* and *obscurus* which are worldwide and grow to a large size, it is clear that such variability is small. By contrast, in a few other species geographic variability is well marked but does not conform to any consistent pattern. Amongst those species which have limited distributions and are small in size, *dussumieri* varies in vertebral numbers in a seemingly random way, whereas amphie-

correlated with water temperatures. Two further species, *brachyurus* and *brevipinna*, which are essentially worldwide and grow to a large size, also differ in the nature of their variability. In *brachyurus* the variability is orderly and appears to be clinal in nature, with the two ends of the cline separated by the mid-Atlantic. In *brevipinna* the variability is less regular geographically, but again the lowest and highest counts occur on opposite sides of the Atlantic, or at least at the western North Atlantic and the eastern Atlantic-Mediterranean (western South Atlantic samples have intermediate counts). This trans-Atlantic difference within each of these two species is manifest, however, in two opposing ways: in *brachyurus* the western Atlantic population has the highest precaudal numbers (matched only by the eastern Pacific) whereas in *brevipinna* the western North Atlantic population has the lowest precaudal numbers.

The striking relationship between vertebral numbers and maximum size in most fishes was skillfully explored and displayed by Lindsey (1975), whose data included most of the counts in the present study. Lindsey showed that for 24 species of *Carcharhinus* there is a strong positive correlation ($r=0.084$; $P<0.001$) between total vertebral count and maximum length. A simple arithmetic plot (Fig. 9) indicates that there is a similar correlation for counts of the two parts of the vertebral column, i.e., for precaudal count and maximum length and also for caudal count and maximum length. However, despite these correlations there is a tendency, as evidenced by Table 2, for small-sized species to have fewer precaudal than caudal vertebrae, whereas the converse holds true for large-sized species. Notable among the exceptions to this tendency are *borneensis*, *cautus*, and *melanopterus* which, although of small size, have more

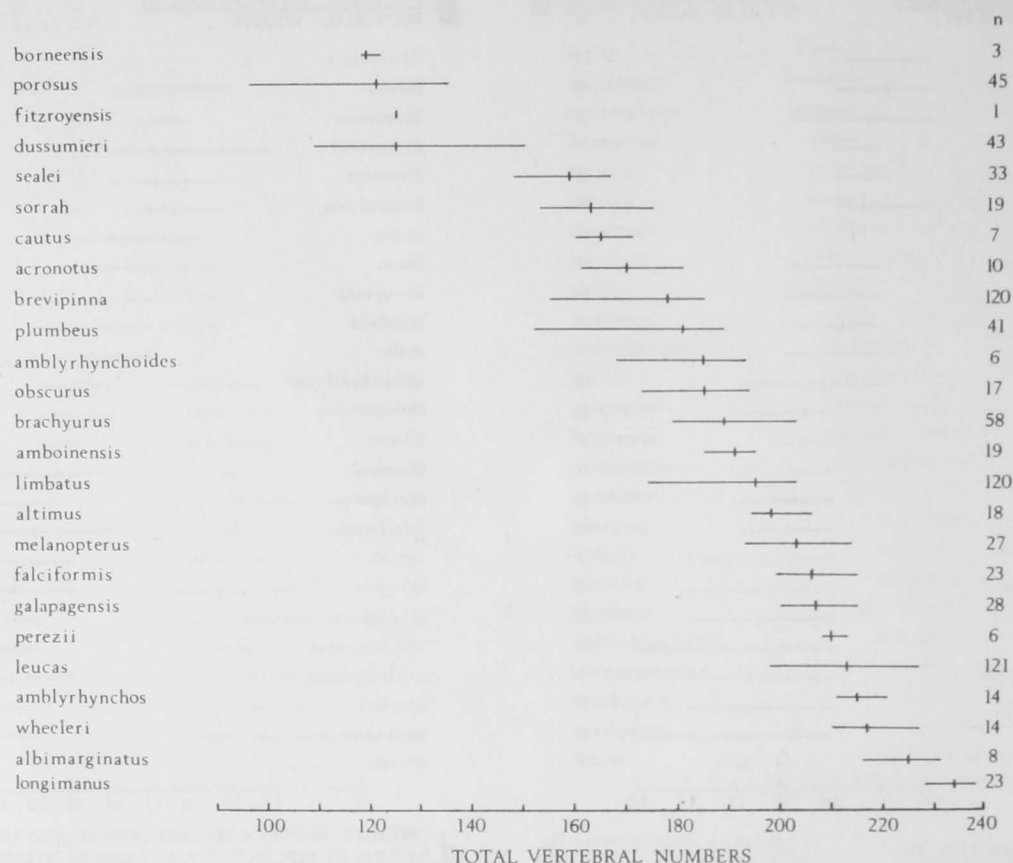


Figure 7.—Proportional dimensions of 25 species of *Carcharhinus*: a, first dorsal fin height divided by length of first dorsal fin rear tip; b, first dorsal fin base divided by length of first dorsal fin rear tip; c, first dorsal fin height divided by second dorsal fin height; d, second dorsal fin rear tip divided by second dorsal fin height (horizontal lines represent ranges; vertical lines are means; n = number of specimens).



Figure 8.—Proportional dimensions of 25 species of *Carcharhinus*: a, second dorsal fin height divided by anal fin height; b, pectoral fin anterior margin divided by pectoral fin width; c, upper caudal lobe length divided by lower caudal lobe length; d, distance between second dorsal fin origin and anal fin origin as percent of total length anterior (negative value) or posterior (positive value) to anal fin origin (horizontal lines represent ranges; vertical lines are means; n = number of specimens).

Table 1.—Total vertebral numbers in 25 species of *Carcharhinus* (horizontal lines represent ranges; vertical lines are means; n = number of specimens).



precaudal than caudal vertebrae, and *obscurus* and *falciformis* which are of large size but have slightly fewer precaudals than caudals.

Carcharhinus species do not differ greatly in their overall body proportions including depth of trunk relative to its length. This relativity must also pertain to the proportions of the vertebral column judging by Figure 10 in which a plot of $\frac{\text{length}}{\text{diameter}}$ of the penultimate monospondylous centrum places

the species in an order closely approximating the inverse of that shown in Table 2 for precaudal numbers. Separation of individual species on this character is limited by the considerable degree of overlap between them, but even so there is far less overlap than in the plot shown in Figure 11 which displays data on $\frac{\text{length}}{\text{length of penultimate monospondylous centrum}}$.

length of first diplospondylous centrum

The position at which diplospondyly begins is rather variable in *Carcharhinus*, not only between species but in many cases within species (Fig. 12). In broad terms the commonest position (14 species) is entirely within the limits of the pelvic base. In six species it ranges farther posteriorly, to or slightly behind the second dorsal fin origin, although including part of the pelvic base or at least the level of the pelvic axil in the range. In three species which are notably dissimilar in other ways (*cautus*, *sorrah*, and *fitzroyensis*), it is entirely behind the pelvic base. Only in *borneensis*, for which I have limited data, is the position clearly anterior to the pelvic origin. I have no data for *amboinensis*.

Finally with respect to vertebrae, I note that although most *Carcharhinus* species have diplospondylous centra which are very regular in appearance (Plate 1) either because adjacent centra are uniform in length (the commonest situation) or alternate

slightly but regularly in length, there are three species (*acronotus*, *dussumieri*, and *sealei*) in which these centra are markedly irregular. The irregularity is due to the presence of elongate centra, frequently corresponding to monospondylous centra in length, being interposed amongst the short diplospondylous centra either singly or in groups (Plate 1). Usually these long centra are precaudal, but in *dussumieri* they may be caudal as well (see Species Accounts). In the three species mentioned, the irregularity is present in at least half of the specimens examined. In a few other species occasional specimens show comparable though less striking irregularities of this nature. Whether such irregularity in centrum length is matched by irregularity in the emergence or spacing of spinal nerves was not examined.

Teeth.—Tooth counts of *Carcharhinus* species are shown in the frequency distribution in Table 4, together with the commonest dental formula for each species. The data are almost exclusively from counts made by me. Because the range in number of teeth for all species combined is small, and many species have counts spread across a sizeable fraction of this range, dental formulae alone do not offer a ready means of identifying species. However, dental formulae combined with tooth shape, and to some degree tooth size, offer much more scope. Differences in tooth shape are particularly evident in the upper teeth which vary in the extent to which they are oblique or upright, in the breadth of their blades, in the shape of their margins, and in the nature of their serrations which may be uniform or larger basally. The lower teeth are less variable, at least in their breadth, most of them being narrow, but in a few species they are distinctive in having smooth rather than serrated

Table 2.—Precaudal and caudal vertebral numbers, and maximum total length in 25 species of *Carcharhinus* (horizontal lines represent ranges; vertical lines are means; n = number of specimens).

porosus		46	46	
fitzroyensis		1	1	
dussumieri		43	42	
borneensis		4	3	
sorrah		21	13	
sealei		36	14	
acronotus		10	10	
brevipinna		122	31	
cautus		10	7	
amblyrhynchoides		7	6	
plumbeus		41	15	
obscurus		119	17	
amboinensis		20	3	
limbatus		123	34	
brachyurus		75	21	
falciiformis		28	23	
altimus		18	2	
perezii		8	6	
galapagensis		30	14	
wheeleri		15	5	
amblyrhynchos		14	14	
melanopterus		28	17	
leucas		151	17	
albimarginatus		22	8	
longimanus		24	9	

40 50 60 70 80 90 100 110 120 130

Precaudal (—) and caudal (---) vertebral numbers

n n

Precaudal Caudal

0 1000 2000 3000

Maximum length (mm)

margins. Complicating the use of these features are firstly, differences between juvenile and adult teeth, at least insofar that juvenile teeth do not fully display the characteristics of adult teeth, and secondly, sexual dimorphism. The extent of sexual dimorphism in *Carcharhinus* has yet to be documented; although it is very obvious in species such as *brachyurus* and *sealei* (see Species Accounts) it probably occurs to a lesser degree in a greater number of species than has so far been recognized.

In summary the teeth are very useful diagnostic features, permitting the ready identification of some species, e.g., *altimus* and *brachyurus*, with a high degree of confidence. In other cases they narrow the possibilities to a few species in which the differences between the teeth are slight and subtle. Ultimate success in recognizing these subtleties, and hence the species, depends on such things as the nature of the teeth, comparative material, the adequacy of illustrative material, and the experience of the

observer. I note that the excellent photographs of the teeth of many *Carcharhinus* species in Bass et al. (1973) provides a very useful reference source.

Middorsal Dermal Ridge.—The presence of a low dermal ridge along the midline between the dorsal fins in some species is an immediately useful feature for distinguishing them from others in which this ridge is absent (Table 5). In 9 species the ridge is always present, and in 11 it is absent except for occasional specimens in which it may occur as an artifact of preservation, perhaps due to drying out or shrinkage. In *longimanus* it is usually but not always present even in fresh specimens, while the converse is true for *amblyrhynchos*, *brachyurus*, and *wheeleri* which are usually smooth backed. The most variable species is *sealei* in which two geographically separated populations differ in the extent to which they possess a ridge.

14

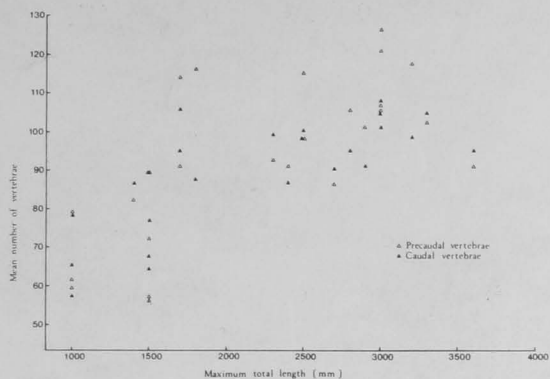


Figure 9.—Relation of mean number of precaudal and caudal vertebrae to maximum total length in 25 species of *Carcharhinus* (each symbol represents a species).

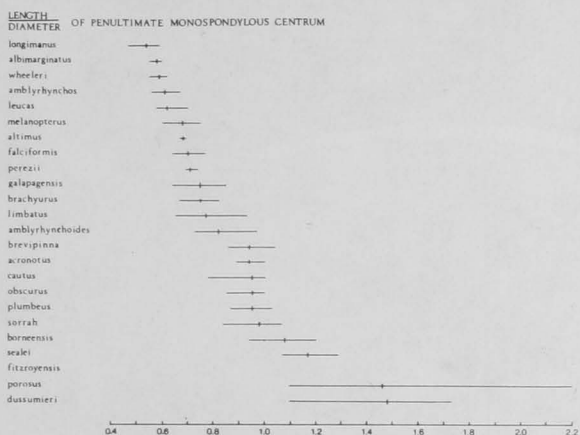


Figure 10.—Length of penultimate monospondylous centrum divided by its diameter in 24 species of *Carcharhinus* (no data for *amboinensis*; horizontal lines represent ranges; vertical lines are means; n = number of specimens).

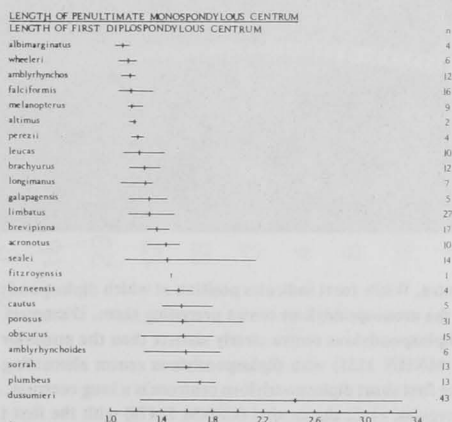


Figure 11.—Length of penultimate monospondylous centrum divided by length of first diplospondylous centrum in 24 species of *Carcharhinus* (no data for *amboinensis*; horizontal lines represent ranges; vertical lines are means; n = number of specimens).

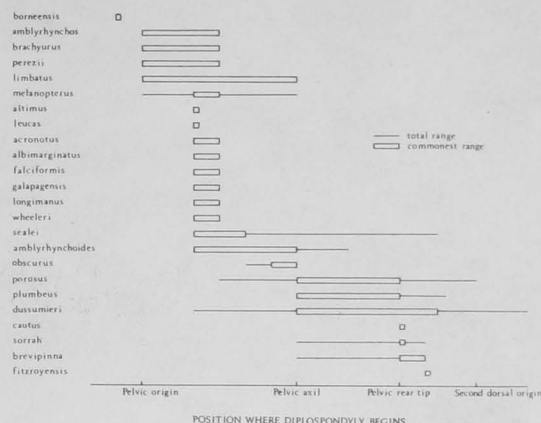


Figure 12.—Position where diplospondyly begins relative to origin, axil, and rear tip of the pelvic fin and origin of second dorsal fin in 24 species of *Carcharhinus* (no data for *amboinensis*).

Color.—Overall body color of *Carcharhinus* species is of little diagnostic value. Although it is true that living or freshly caught specimens of different species are often clearly separable by color, it is equally true that accounts by different authors of the color of fresh specimens of the same species often differ markedly. Postmortem changes in color, or changes due to bleaching by sunlight or from preservation in Formalin or alcohol reduce the color of most specimens to various hues of drab gray, grayish brown, or brown above and white or paler below, leaving little scope for discrimination.

The presence of a color pattern, involving dusky to black, or white, markings on the fin tips and fin margins is, however, of great importance in recognizing many species. Such markings can also be subject to postmortem change or fading, and in some species they vary not only with size (or age) of the specimen but also geographically. For these reasons they need to be used with caution in all except a few species where they are so distinctive and well developed that they are not easily misinterpreted.

With respect to a pattern of white markings, only two species obviously fit this category, these being *albimarginatus* in which the tips and trailing margins of all fins are white, and *longimanus* in which most, and sometimes all, fins are white marked but not uniformly so, being mottled with grayish brown. Newborn and juvenile *longimanus* in addition have black tips or blotches on most fins and on the dorsum of the posterior half of the trunk, but these fade and are largely absent in adults. The only other species in which a white fin marking is important in diagnosis is *wheeleri*, in which the apex and trailing margin of the first dorsal is white. However, in *wheeleri* all the other fins are dusky to black tipped, and it is the combination of these black markings, particularly the prominent black edge on the trailing margin of the caudal, and the white-tipped first dorsal, which is significant.

The value of patterns involving black markings is limited to some extent by the fact that all except one of the remaining species may have dusky or dark fin tips. The exception is *fitzroyensis*, so far known only from two specimens, in which the fins have no obvious dark markings. The chief problem is in differentiating between those species with prominent and consistent markings, usually black rather than dusky, and those with less definite, frequently inconsistent dusky markings. In the latter group can be placed 10 species in which dusky marks may be present on some or most of the fin tips, but nearly always on the

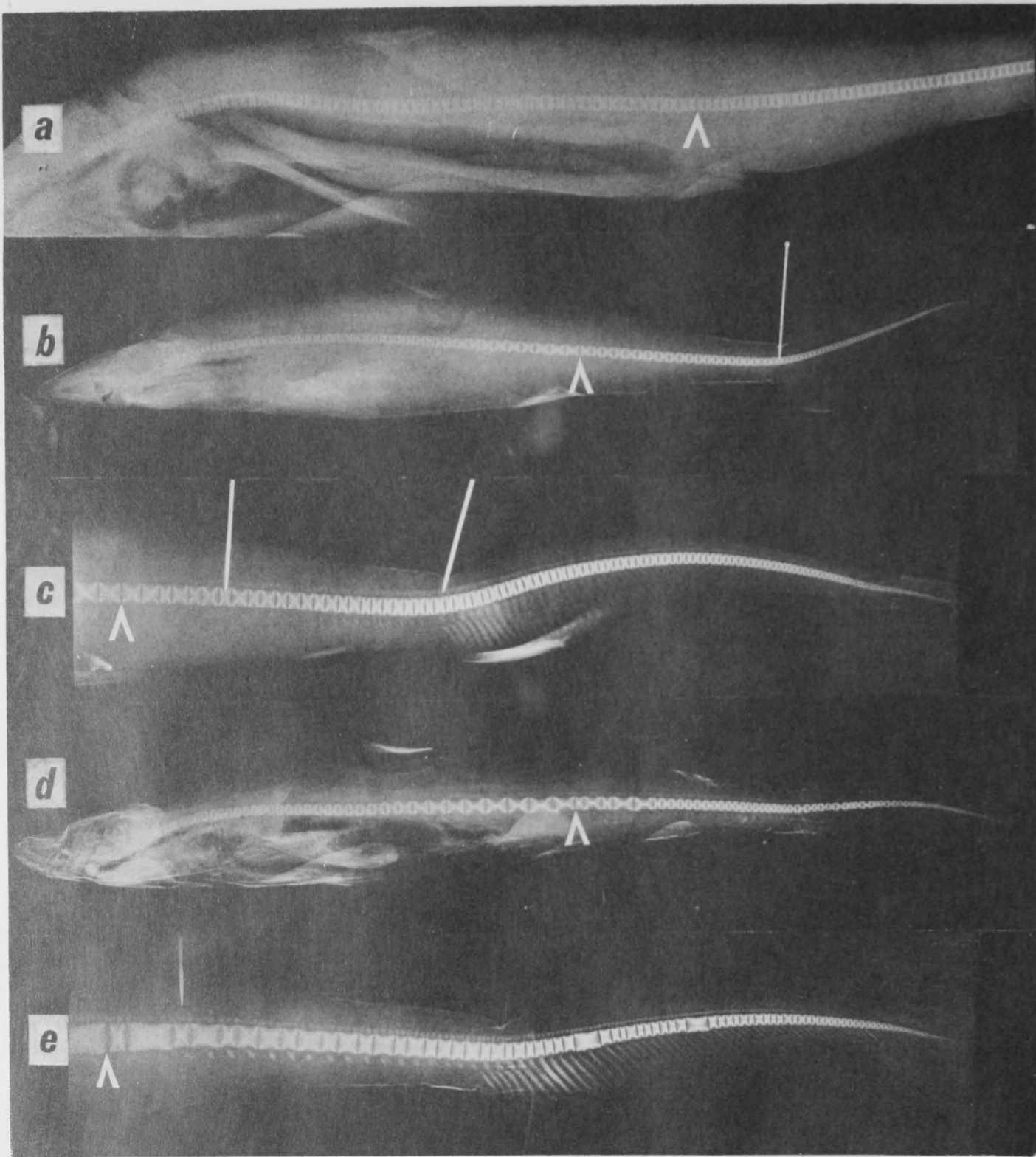


Plate 1.—Radiographs of *Carcharhinus* species showing variation in the nature of the diplospondylous centra. White caret indicates position at which diplospondyly begins. a) *C. wheeleri* (MNHN 8001) with diplospondylous centra uniform in length and only slightly shorter than the monospondylous centra preceding them. Diameters of posterior monospondylous centra notably greater than their lengths. b) *C. porosus* (USNM 82707) with uniform diplospondylous centra clearly shorter than the posterior monospondylous centra. Diameters of posterior monospondylous centra are less than their lengths. c) *C. sorrah* (MNHN 1131) with diplospondylous centra alternating slightly but regularly in length. d) *C. dussumieri* (MCZ 1386) with diplospondylous centra irregular in length. Behind the first short diplospondylous centrum is a long centrum, then a short one, then two long ones which precede a series of short precaudal centra. Caudal centra likewise are irregular. e) *C. dussumieri* (USNM 72478) with the first two pairs of diplospondylous centra alternating strikingly in length, and with two very long caudal centra interposed amongst others of short but varying lengths.

Fig. 4.—Frequency distribution of tooth numbers, and commonest dental formula in 26 species of *Channina*.

borneensis	2 6	4	7 1	1 3	$\frac{12-1-12}{11-1-11}$
amboinensis	2 8	5	1 9	5	$\frac{12-1-12}{11-1-11}$
acronotus	16	1 7	14	8	$\frac{12-2-12}{11-1-11}$
sorrah	29 1	12 1 2	4 26	14 1	$\frac{12-1-12}{12-1-12}$
melanopterus	12 6	1 8	4 11 3	1 1 7	$\frac{12-2-12}{11-3-11}$
sealei	18 10	1 4 9	2 24 2	1 12 1	$\frac{12-2-12}{12-1-12}$
perezii	3 15	8 1	2 16	9	$\frac{13-1-13}{12-1-12}$
cautus	4 6 2	1 5	2 5 5	5 1	$\frac{12 \text{ or } 13-2-12 \text{ or } 13}{12 \text{ or } 13-1-12 \text{ or } 13}$
leucas	8 39 2	25	43 6	23 2	$\frac{13-1-13}{12-1-12}$
dussumieri	18 110 4	2 11 49 4	1 22 57 47 4	6 57 3	$\frac{13-2-13}{13 \text{ or } 14-1-13 \text{ or } 14}$
albimarginatus	1 17 2	9 1	13 5 2	7 3	$\frac{13-1-13}{12-1-12}$
wheeleri	8	3 1	6 2	4	$\frac{13-1-13}{12-1-12}$
amblyrhynchos	10 20	14 1	25 5	15	$\frac{14-1-14}{13-1-13}$
plumbeus	2 28	15	4 14 12	13 2	$\frac{14-1-14}{13 \text{ or } 14-1-13 \text{ or } 14}$
porosus	8 17 5	13 2	1 13 13 3	8 3 4	$\frac{14-1-14}{13 \text{ or } 14-0-13 \text{ or } 14}$
galapagensis	2 34 4	17 2 1	10 25 4	18 1 1	$\frac{14-1-14}{14-1-14}$
fitzroyensis	4	2	2 2	2	$\frac{14-2-14}{13 \text{ or } 14-2-13 \text{ or } 14}$
longimanus	21	3 7	3 17 1	8 1 1	$\frac{14-2-14}{14-1-14}$
obscurus	30 15	12 11	7 32 2	13 8	$\frac{14-1 \text{ or } 2-14}{14-1-14}$
falciformis	4 32 16	9 12 5	4 29 16 1	19 6 1	$\frac{15-2-15}{15-1-15}$
limbatus	2 64 2	1 26 7	8 48 12	5 14 14	$\frac{15-2-15}{14-2 \text{ or } 3-14}$
brachyurus	1 37 31	5 20 10	18 50	27 5 3	$\frac{15 \text{ or } 16-2-15 \text{ or } 16}{15-1-15}$
amblyrhynchoides	12	1 3 2	7 5	3 1 2	$\frac{15-2-15}{14 \text{ or } 15-1-14 \text{ or } 15}$
altimus	20 10	9 6	16 14	15	$\frac{15-1-15}{14 \text{ or } 15-1-14 \text{ or } 15}$
brevipinna	1 35 15 1	23 3	2 24 15 11	22 2 2	$\frac{16-2-16}{15 \text{ or } 16-1-15 \text{ or } 16}$
	$\frac{11}{12} \frac{13}{14} \frac{15}{16} \frac{17}{18}$	$\frac{0}{1} \frac{2}{3}$	$\frac{10}{11} \frac{12}{13} \frac{14}{15} \frac{16}{17}$	$\frac{0}{1} \frac{2}{3}$	COMMONEST FORMULA
	Laterals	Symphysials	Laterals	Symphysials	
	UPPER TEETH		LOWER TEETH		

Table 5.—Occurrence of middorsal dermal ridge in *Carcharhinus* species.

Species	Present	Usually present	Usually absent	Absent
<i>albimarginatus</i>	X			
<i>altimus</i>	X			
<i>dussumieri</i>	X			
<i>falciformis</i>	X			
<i>galapagensis</i>	X			
<i>obscurus</i>	X			
<i>perezii</i>	X			
<i>plumbeus</i>	X			
<i>sorrah</i>	X			
<i>sealei</i>		X ¹	X ²	
<i>longimanus</i>		X		
<i>amblyrhynchos</i>			X	
<i>brachyurus</i>			X	
<i>wheeleri</i>			X	
<i>acronotus</i>				X
<i>amblyrhynchoides</i>				X
<i>amboinensis</i>				X
<i>borneensis</i>				X
<i>brevipinna</i>				X
<i>cautus</i>				X
<i>fitzroyensis</i>				X
<i>leucas</i>				X
<i>limbatus</i>				X
<i>melanopterus</i>				X
<i>porosus</i>				X

¹Eastern Indian Ocean—western Pacific specimens.

²Western Indian Ocean specimens.

pectoral and lower caudal, and generally not on the first dorsal. Juveniles of these species usually have more definite markings than adults. Nine of these 10 species are large sharks (*altimus*, *amboinensis*, *brachyurus*, *falciformis*, *galapagensis*, *leucas*, *obscurus*, *perezii*, *plumbeus*) but the tenth is the small *porosus* which further differs from the others in sometimes having a dusky margined first dorsal fin.

Contrasting with the above are 12 species with much more definite dark markings. In four of these the markings are very restricted in position. In *dussumieri* and *sealei* only the second dorsal is black tipped, all other fins being pale. In *acronotus* the second dorsal is similarly though less obviously marked, but as well the caudal margins are usually dark, and in most, perhaps all specimens in life, there is a dark blotch on the snout tip. In *borneensis* the first dorsal tip is dark and the upper caudal has a dusky margin. In the remaining eight species the markings are much more extensive, involving several fins. Two of these species (*amblyrhynchos* and *wheeleri*) are notable in having a prominent, wide black edging along the trailing margin of the caudal as well as dark tips or margins on most or all of the other fins except the first dorsal which is either essentially plain colored (*amblyrhynchos*) or distinctly white tipped (*wheeleri*). The other six species (*amblyrhynchoides*, *brevipinna*, *cautus*, *limbatus*, *melanopterus*, and *sorrah*) have various combination of black-tipped or black-margined fins (see Species Accounts) which are diagnostic for some of them, though *amblyrhynchoides*, *limbatus*, and *brevipinna* are very similar in their markings. An unusual feature of *brevipinna* is that its black markings are not present at birth but progressively develop in juveniles. Data for *limbatus* show that the shape of the black tip on the underside of the pectoral fin varies throughout some parts of the geographical range of this species. The two species in which the black fin tips are most strikingly developed are *melanopterus* and *sorrah*.

Dermal Denticles.—Brief descriptions of the dermal denticles are given in the species accounts but I find that they are of little practical value in identifying species. Basically the denticles are very similar in shape in all *Carcharhinus* species, and differences between species are usually less than those between growth stages of the same species. Some species have been described as having nonimbricate denticles, in contrast to others with overlapping denticles [see Springer (1960) who places *plumbeus* and *altimus* in the former category], but although this is generally true, the usefulness of this criterion is reduced by the fact that the young of several very dissimilar species (*amboinensis*, *borneensis*, *cautus*, *leucas*, and *porosus*) can have loose-spaced denticles whereas in the adults they are overlapping—and this applies also to *altimus* where specimens greater than 1.5 m long have overlapping denticles.

Biology.—Various aspects of the biology of *Carcharhinus*—in particular maximum size, size at first maturity, size at birth, and number of embryos per litter—show differences between the species as indicated in Figure 13. However, it must be stressed that data for these parameters are in many cases very sparse and subject to variability from several causes. In at least some species, e.g., *plumbeus*, populations in parts of the geographical range show differences in these parameters. In most species data for maximum size indicate differences between the sexes, with females being larger than males. Also in those species for which data are relatively numerous there are occasional records of specimens reaching a much larger size than the many others in the samples. For these reasons, plus the possibility of misidentifications in some literature accounts, the data in Figure 13 can only be regarded as approximations, rather crude in many cases, of what may be found in any particular sample studied.

Maximum size as given in Figure 13 does not take account of sex, but generally speaking it is based on females. Separate data on males and females are presented in the species accounts. Maximum size ranges from about 1 to 3.6 m. On average males attain a maximum size about 7% smaller than females, but variation around this is considerable, and for all species the males range from about 2 to 14% smaller than the females. Mean data for each species on size at first maturity produces a plot for the genus as a whole that parallels that of maximum size. On average for both sexes combined first maturity is reached at about 70% of maximum size. Again, males achieve this at a



Figure 13.—Number of embryos per litter, size at birth, size at first maturity, and maximum size in 24 species of *Carcharhinus* (no data for *fitzroyensis*).

smaller size than females, the difference between the sexes averaging about 5% of maximum size. The spread, however, is considerable, even using mean species data. Thus for males first maturity size ranges from about 50 to 85% of maximum size, while for females it is about 60 to 90%.

Mean values for each species for relative size at birth range from about 22 to 39% of maximum size and average about 27%. Actual size at birth ranges from 250 to 1,000 mm. The relationship between birth size and maximum size is influenced by variation in the number of embryos per litter. The latter ranges from 1 to 23 (Fig. 13) and, as shown in Figure 14, there is a reasonably good inverse relationship between this number and size at birth as a percentage of maximum size. Species with the largest litters, as, for example, those seven species which have a median litter number of not less than 8 (actual litter range between 1 and 23) are all of large maximum size, averaging 3.1 m long (range 2.7-3.6 m). Conversely, species with the smallest litters, such as seven with a median litter number of not more than four (actual litter range between one and six) are mostly of small to moderate maximum size, averaging 1.8 m long (range 1.0-3.0 m).

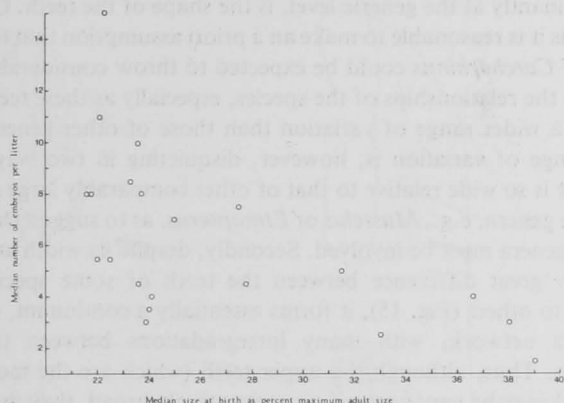


Figure 14.—Relation of median number of embryos per litter to median size at birth as percent of maximum adult size in 21 species of *Carcharhinus* (no data for *amblyrhynchoides*, *borneensis*, *cautus*, and *fitzroyensis*).

The above data contribute to our knowledge of the species, but they have little positive value, other than giving corroboration, for identifying species. They have some predictive value for species for which biological data are very incomplete. However, an equally important use is in providing evidence for rejecting or casting doubt on some literature identifications which are not supported by descriptions or illustrations but which are accompanied by comments on various aspects of size or biology.

GENERIC SYNONYMY

Carcharhinus Blainville, 1816:121. Type species *Carcharias melanopterus* Quoy and Gaimard, 1824, by designation under the plenary powers of the International Commission on Zoological Nomenclature, Opinion 723, 1965:32; placed on official List of Generic Names in Zoology under same Opinion [Name No. 1657].

Galeolamna Owen, 1853:96. Type species *Galeolamna greyi* Owen, 1853, by monotypy; treated in present account as

species dubia although genus seems referable to *Carcharhinus*.

Eulamia Gill, 1862:399, 401, 409-410. Type species *Carcharias (Prionodon) milberti* Valenciennes in Müller and Henle, 1841, as listed by Gill on p. 410, by monotypy because the *Eulamia lamia* Gill listed by Gill as type species on p. 401 was a nomen nudum; junior synonym of *Squalus plumbeus* Nardo, 1827.

Platyposdon Gill, 1862:401. Type species *Carcharias (Prionodon) menisorrah* Valenciennes in Müller and Henle, 1841, by original designation; equals *Carcharias (Prionodon) falciformis* Bibron in Müller and Henle, 1841, following lectotype designation for it in present account.

Isoplagiodon Gill, 1862:400, 401, 410. Type species *Carcharias (Prionodon) sorrah* Valenciennes in Müller and Henle, 1841, by original designation.

Gymnorhinus Hemprich and Ehrenberg, 1899:8 (but spelt *Gymnorhinus* on pl. 7). Two included species, *G. pharaonis* [equals *Carcharias (Prionodon) falciformis* Bibron in Müller and Henle, 1841] and *G. abbreviatus* [equals *Carcharias (Prionodon) limbatus* Valenciennes in Müller and Henle, 1841]; preoccupied by *Gymnorhinus* Wied, 1841, a bird.

Mapolamia Whitley, 1934:185, 188. Type species *Carcharias melanopterus* Quoy and Gaimard, 1824, by original designation.

Gillisqualus Whitley, 1934:185, 189. Type species *Gillisqualus amblyrhynchoides* Whitley, 1934, by original designation.

Galeolamnoides Whitley, 1934:185, 191. Type species *Carcharias macrurus* Ramsay and Ogilby, 1887a, by original designation; equals *Squalus obscurus* Lesueur, 1818.

Longmania Whitley, 1939:231. Type species *Carcharias (Aprion) brevipinna* Müller and Henle, 1841, by original designation.

Uranga Whitley, 1943:115. Type species *Uranga nasuta* Whitley, 1943, by original designation; equals *Carcharias (Aprion) brevipinna* Müller and Henle, 1841.

Uranganops Whitley, 1943:117. Subgenus of *Galeolamna*: type species *Galeolamna (Uranganops) fitzroyensis* Whitley, 1943, by original designation.

Lamnarius Whitley, 1943:119. Subgenus of *Galeolamna*: type species *Carcharias spenceri* Ogilby, 1910, by original designation; equals *Carcharias (Prionodon) leucas* Valenciennes in Müller and Henle, 1841.

Ogilamia Whitley, 1943:122. Subgenus of *Galeolamna*: type species *Galeolamna (Ogilamia) stevensi* (Ogilby, 1911), by monotypy; equals *Squalus plumbeus* Nardo, 1827.

Bogimba Whitley, 1943:123. Subgenus of *Galeolamna*: type species *Galeolamna (Bogimba) bogimba* Whitley, 1943, by original designation; equals *Carcharias (Prionodon) leucas* Valenciennes in Müller and Henle, 1841.

Pterolamia Springer, 1950:7. Type species *Squalus longimanus* Poey, 1861; preoccupied by *Pterolamia* Breuning, 1942, a beetle; placed on Official Index of Rejected and Invalid Generic Names in Zoology [Name No. 1752] by International Commission on Zoological Nomenclature, Opinion 723, 1965:33.

Pterolamiops Springer, 1951:244. Type species *Squalus longimanus* Poey, 1861, by original designation, through *Pterolamia* Springer, 1950; placed on Official Index of Generic Names in Zoology [Name No. 1661] by International Commission on Zoological Nomenclature, Opinion 723, 1965:32.

GENERIC DIAGNOSIS

Carcharhinidae [in the sense of the "advanced carcharhinids" of Compagno (1970)] with an internal nictitating lower eyelid; no spiracles or at most they are occasionally present in juveniles as minute vestiges; short labial furrows, the length of each less than 1% TL, the lower scarcely or not visible when mouth is closed; snout short to moderately long but the preoral length always less than 10% TL; internarial distance at least 2.5 times nostril width; teeth bladelike with single cusps, though the basal margins of the cusps may have enlarged serrae; cusps of upper teeth serrated towards their tips as well as basally; cusps of lower teeth serrated or smooth; total number of teeth in row around upper or lower jaw not exceeding 40 and usually less than this number; midpoint of first dorsal base at least as near, and usually nearer, to pectoral axil than to pelvic origin; vertical height of second dorsal fin never more than 55% of height of first dorsal, and from 60 to 120% of height of anal fin; second dorsal fin more or less above anal fin, its origin usually in front of midpoint of anal base but exceptionally over posterior third of anal base; upper and lower precaudal pits present, the upper better developed, crescent-shaped, wider than long, with a well-marked anterior edge or border; caudal peduncle without lateral dermal ridges.

INTRAGENERIC RELATIONSHIPS OF CARCHARHINUS SPECIES

Some Species Groups

Previous attempts to subdivide the genus *Carcharhinus* have not been successful. Proposals by Owen (1853), Gill (1862), Whitley (1934, 1939, 1943), and Springer (1950, 1951) made names available for 14 additional genus-group taxa for nominal species here included in *Carcharhinus*. Taking into account that some of these are synonyms, the remainder have as their type species 10 (or 40%) of the 25 species treated here as valid (Table 6). These genus-group taxa were defined on various criteria. Owen (1853) based his *Galeolamna* on dental characteristics. Gill (1862) diagnosed *Eulamia*, *Platypodon*, and *Isoplagiodon* mainly on tooth shape but with some reference to fin positions. Whitley (1934, 1939, 1943) used a wider range of features for the nine genera or subgenera he proposed, including snout length and shape, tooth shape and number, fin positions, and in some cases the presence or absence of a middorsal ridge. Springer (1950, 1951) defined *Pterolamiops* principally on the presence of

a middorsal ridge coupled with rounded tips to the first dorsal and pectoral fins.

Perhaps the prime reason for these taxa failing to become established in usage is that for the most part they were erected on the basis of only one species for each and without sufficient reference to, or distinction from, other known species. I do not imply criticism in this statement—the poor state of knowledge of *Carcharhinus* species in general did not allow meaningful comparison in many cases. The main exception to the above is Springer's (1950, 1951) treatment of *Pterolamiops* in which he surveyed a wide range of species and concluded that *Carcharhinus* s.l. could be subdivided into smooth-backed species (*Carcharhinus* s.s.) and ridge-backed forms, with the latter in turn subdivisible into those with pointed first dorsal and pectoral tips (*Eulamia*) and those with rounded tips (*Pterolamiops*). The failure of this treatment stemmed from subsequent realization that both his ridge-backed (*Eulamia*) group and his smooth-backed group contained species too diverse in other features to be aligned with each other.

If one takes an overview of shark systematics in general, the best single feature that could be cited for determining similarities and differences between taxa at all levels, but perhaps predominantly at the generic level, is the shape of the teeth. On this basis it is reasonable to make an a priori assumption that the teeth of *Carcharhinus* could be expected to throw considerable light on the relationships of the species, especially as these teeth display a wider range of variation than those of other genera. This range of variation is, however, disquieting in two ways. Firstly it is so wide relative to that of other comparably large or speciose genera, e.g., *Mustelus* or *Etmopterus*, as to suggest that several genera must be involved. Secondly, despite its width and the very great difference between the teeth of some species relative to others (Fig. 15), it forms essentially a continuum, or rather a network, with many intergradations between the extremes. Thus, although the upper teeth (which are the most variable) may be very narrow, or contrastingly broad, they may also be of intermediate, moderate breadth. A similar lack of discontinuity applies to other of their features, including the shape of the tooth margins (straight, concave, notched, or sinuous), the serrations on the margins (of uniform size or enlarged basally), and whether the teeth are erect or oblique. The consequence of this is that it is virtually impossible to categorize discrete tooth types into which the species can be grouped with confidence. The best that can be done is to recognize nodes of diversity in tooth shape which exemplify the several extremes

Table 6.—Available genus-group names for *Carcharhinus* species.

Name	Type species	Identity of type species
<i>Galeolamna</i> Owen, 1853	<i>Galeolamna greyi</i> Owen	Species dubium (poss. <i>falciformis</i> or <i>obscurus</i>)
<i>Eulamia</i> Gill, 1862	<i>Carcharias (Prionodon) milberti</i> Val.	<i>plumbeus</i> Nardo
<i>Ogilamia</i> Whitley, 1943	<i>Carcharhinus stevensi</i> Ogilby	<i>plumbeus</i> Nardo
<i>Platypodon</i> Gill, 1862	<i>Carcharias (Prionodon) menisorrh</i> Val.	<i>falciformis</i> Bibron
<i>Isoplagiodon</i> Gill, 1862	<i>Carcharias (Prionodon) sorrah</i> Val.	<i>sorrah</i> Val.
<i>Mapolamia</i> Whitley, 1934	<i>Carcharias melanopterus</i> Q. & G.	<i>melanopterus</i> Q. & G. (= type species of <i>Carcharhinus</i> Blainville, 1816)
<i>Gillisqualus</i> Whitley, 1934	<i>Gillisqualus amblyrhynchoides</i> Whitley	<i>amblyrhynchoides</i> Whitley
<i>Galeolamnoides</i> Whitley, 1934	<i>Carcharias macrurus</i> Ramsay & Ogilby	<i>obscurus</i> Le Sueur
<i>Longmania</i> Whitley, 1939	<i>Carcharias (Aprion) brevipinna</i> M. & H.	<i>brevipinna</i> M. & H.
<i>Uranga</i> Whitley, 1943	<i>Uranga nasuta</i> Whitley	<i>brevipinna</i> M. & H.
<i>Uranganops</i> Whitley, 1943	<i>Galeolamna (Uranganops) fitzroyensis</i> Whitley	<i>fitzroyensis</i> Whitley
<i>Lamnarius</i> Whitley, 1943	<i>Carcharias spenceri</i> Ogilby	<i>leucas</i> Val.
<i>Bogimba</i> Whitley, 1943	<i>Galeolamna (Bogimba) bogimba</i> Whitley	<i>leucas</i> Val.
<i>Pterolamiops</i> Springer, 1951	<i>Squalus longimanus</i> Poey	<i>longimanus</i> Poey

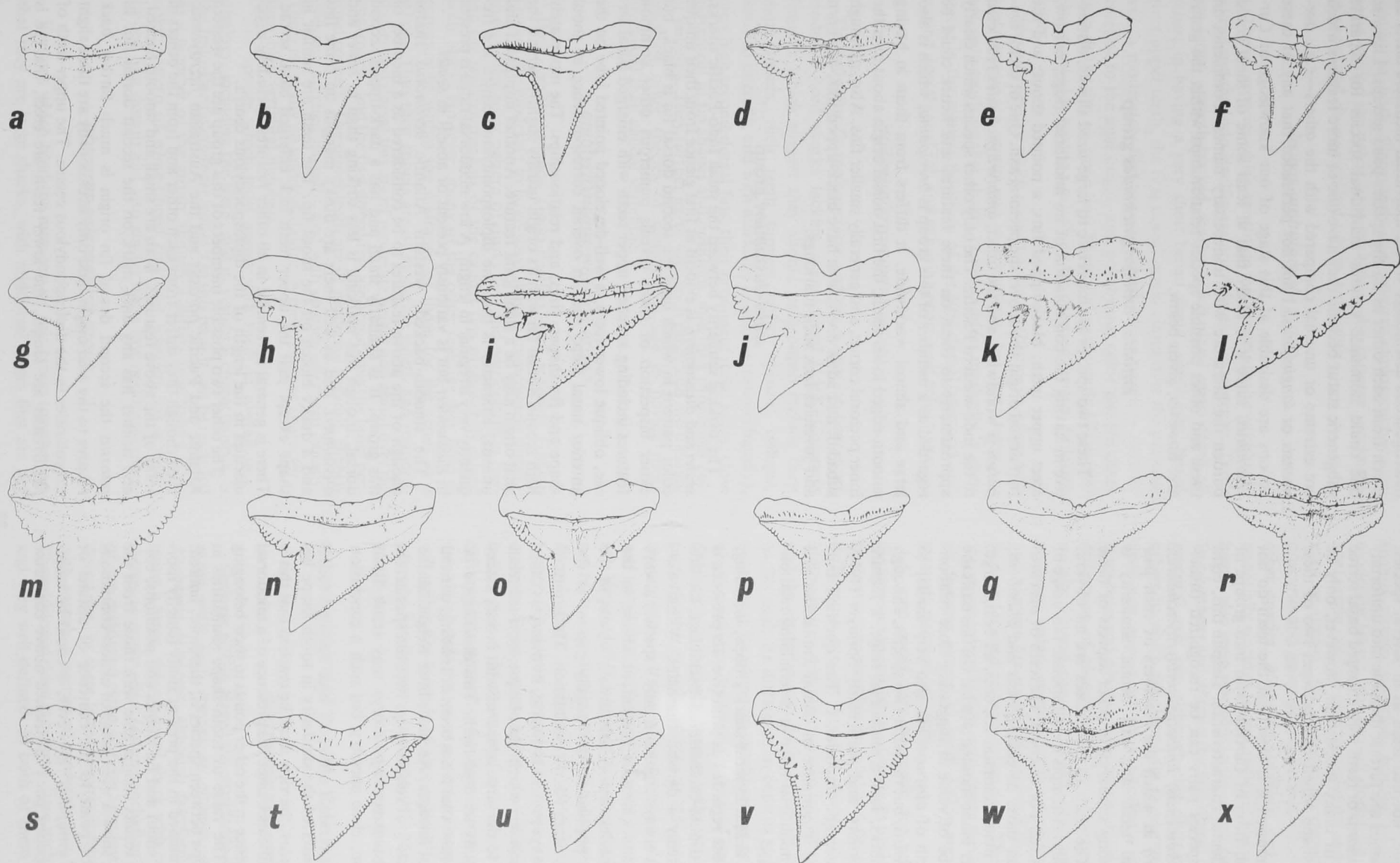


Figure 15.—Upper tooth shape as exemplified by fifth upper tooth in 24 species of *Carcharhinus* (*amboinensis* not shown): a, *brevipinna*; b, *limbatus*; c, *amblyrhynchoides*; d, *wheelerti*; e, *amblyrhynchus*; f, *melanopterus*; g, *acronotus*; h, *porosus*; i, *borneensis*; j, *sealei*; k, *dussumieri*; l, *cautus*; m, *fitzroyensis*; n, *sorrah*; o, *albimarginatus*; p, *falciformis*; q, *perezii*; r, *brachyurus*; s, *longimanus*; t, *leucas*; u, *obscurus*; v, *galapagensis*; w, *plumbeus*; x, *altimus*.

that are present. Obvious examples of such nodes are narrow, erect teeth as in *limbatus*, broad, essentially erect teeth as in *longimanus*, and oblique, notched teeth as in several species, though these last mentioned are further divisible into uniformly serrated teeth as in *acronotus* or teeth with enlarged basal serrae as in *sealei*. The teeth of many species can, however, only be described as having a shape which falls between two of these nodes.

From the above comments it is clear that the teeth do not allow an unequivocal division of *Carcharhinus* into groups of species with common dental characteristics. Despite this, eight species forming four species pairs can be recognized (*sealei-dussumieri*; *leucas-ambloinensis*; *limbatus-amblyrhynchoides*; *amblyrhynchos-wheeleri*) in which the members of each pair have virtually identical teeth and this dental similarity is matched by equally strong similarity in other aspects of these species' morphology. The teeth in these cases are an obvious index of close relationship. Attempts to extrapolate this usage of the teeth are less successful. For example, the teeth of *obscurus* differ only slightly from those of *galapagensis* and *plumbeus*, and these species share many common features, all being large, ridge-backed, and rather blunt-snouted sharks. On this basis the teeth again appear to be of value in suggesting close relationship. However, the teeth of *obscurus* are also very similar to those of *leucas-ambloinensis*, but the latter two species, although large, blunt-snouted sharks, lack a middorsal ridge, a feature regarded by several authors, and particularly Springer (1950, 1960), as of prime systematic importance. The question thus arises as to the relative importance of dental similarities and presence/absence of a middorsal ridge in determining relationships between the species.

A middorsal ridge is absent in most shark groups, including, as far as I know, all those regarded as primitive. Its presence is best documented in the triakid-carcharhinid assemblage. On this evidence it is undoubtedly a derived character. Within *Carcharhinus* (Table 5) it is always present in only 9 species, always absent in 11 species, and variously present or absent in the remaining 5. In one species (*sealei*) it is usually absent in the western Indian Ocean population but usually present in the eastern Indian Ocean-western Pacific population. The group of species in which it is always present is diverse, its members ranging from the small *dussumieri* which has oblique, notched teeth with large basal serrae to the large *obscurus* with broad, essentially erect, and uniformly serrated teeth. This distribution of the middorsal ridge suggests that it has been, or is being, derived independently in several lineages. As such, little weight can be placed on it as an indicator of relationships between species. Its presence in *obscurus-galapagensis-plumbeus* may result from their sharing a common, close ancestry, but such a conclusion would be arbitrary.

Returning to the matter of the similarity in tooth shape between *obscurus* and *leucas*, the view must be reached that this is of little immediate significance since the presence of a middorsal ridge in one and its absence in the other points to their belonging in different lineages. The value of tooth-shape similarities in determining relationships between species is, therefore, limited.

Other characters examined in the present study (chiefly morphometrics, vertebrae, snout and fin shapes and positions, color, and biology) yield results comparable with those from the teeth, i.e., they mainly show a wide range of almost continuous variation. They do not point to the existence of distinct or substantial subgeneric groupings. However, it could be maintained that the four species pairs mentioned above constitute

potential or even actual subgeneric taxa, but to recognize these formally would still leave the bulk of the species in one heterogeneous assemblage whose individual members differ as much from each other as do the species-pairs groups. Likewise one could nominate various individual species for separate subgeneric status because they have one or more features which are extreme or unusual compared with the others—e.g., *borneensis* or *longimanus*. I am not persuaded that any of these actions are desirable at this stage of our knowledge of *Carcharhinus*, since it is likely that at least some of them could burden the literature with unnecessary names. Comments on these and other possible species relationships within the genus are, however, given below.

limbatus-amblyrhynchoides group

These two species are moderate to large-sized sharks, distinctive in having the combination of no middorsal ridge; narrow, erect upper teeth; black-tipped fins; a pointed snout; and the first dorsal origin about over the pectoral axil. One of them, *limbatus*, is worldwide, and the other, *amblyrhynchoides*, restricted to the Indo-western Pacific. The only other species which clearly approximates to them on these features and hence could be regarded as a member of this group is *brevipinna*, which is also large and almost worldwide. It differs from them in having smooth-edged lower teeth, the first dorsal origin about over the inner pectoral corner, and generally smaller fins. Also, although subadult and adult *brevipinna* have black-tipped fins, newborn and juveniles lack such markings.

sealei-dussumieri group

The striking similarity between the small Indo-Pacific sharks, *sealei* and *dussumieri*, is evident at first glance from their unique color pattern in which only the second dorsal fin is black, but closer inspection of them reveals numerous other common features including notched upper teeth with enlarged basal serrae, oblique lower teeth, a well-developed pointed lobe on the anterior nasal flap, and an overall correspondence in snout shape and fin shapes, sizes, and relationships. The moderately high second dorsal fin with its origin usually slightly behind the anal origin may be a significant feature. Another important and unusual character is that the diplospondylous centra are frequently very irregular in length. A low middorsal ridge is present in *dussumieri* but is variously present or absent in *sealei*.

The smooth-backed, western Atlantic *acronotus* shares enough of the above features to be considered as a member of this group. It is similarly small and has a dark-tipped second dorsal, though this marking is less striking than in *sealei* and *dussumieri*, and as well there are dusky margins on some fins and a dusky blotch on the snout tip. The teeth are similar in shape except that the upper teeth lack enlarged basal serrae. There is general agreement in all other features, including irregularities in the length of the diplospondylous centra.

The other two possible members of this group are the western Atlantic and Pacific *porosus* and the Australian *fitzroyensis*, even though they differ from each other and from the others in some of the above features. Both are small and smooth backed, and neither has any dark mark on the second dorsal fin. In *porosus* the second dorsal fin origin is much farther back relative to the anal origin, and only occasionally are there slight irregularities in the diplospondylous centra. The upper teeth of *fitzroyensis* are longer, the lower teeth are erect, the eye is

smaller, and in the single specimen that could be radiographed the diplospondylous centra alternated slightly but regularly in length. In both *fitzroyensis* and *porosus* diplospondyly can begin behind the pelvic base, as it does also in some specimens of *sealei* and *dussumieri* but not in *acronotus*.

leucas-amboinensis group

The two species which constitute this group are the worldwide *leucas* and the Indo-Pacific-eastern Atlantic *amboinensis*. These are large, smooth-backed sharks which stand apart from all others in having a very short broad snout, small eyes, broad erect upper teeth, the first dorsal origin about over the pectoral axil, a moderately high second dorsal whose origin is notably anterior to the anal origin, and no obvious color pattern other than dusky tips on some fins. They, and particularly *leucas*, are also unusual in having a proclivity for entering fresh or brackish water.

The only species which show much resemblance to *leucas* and *amboinensis* are *cautus* and *melanopterus*, but these latter are not only much smaller sharks but also differ markedly in their teeth, in the relative positions of the first dorsal/pectoral and second dorsal/anal fin, and in having prominent color patterns.

melanopterus-cautus group

The Indo-Pacific *melanopterus* and the Australian *cautus* are moderate-sized sharks lacking a middorsal ridge. Common features which suggest they should be grouped include their short snouts, their teeth (uppers rather narrow, oblique, notched laterally, and with markedly coarser serrations basally), their high second dorsal fins, their prominent nasal lobes, close agreement in fin shapes and positions, and their prominent color patterns. They further agree with each other and are unusual amongst other species of comparable size in having more precaudal than caudal vertebrae.

amblyrhynchos-wheeleri group

Both *amblyrhynchos* (Indo-Pacific) and *wheeleri* (Indian Ocean) are moderate to large-sized sharks, immediately distinctive in their color pattern of dusky fins and particularly in having the trailing margins of the caudal fins prominently edged with black. However, many of the other features they hold in common lie within the midrange of those for the genus as a whole. Thus their snouts are of moderate length and rounded, the second dorsal fins are of moderate height and about over the anal origin, and the first dorsal fins are about over the inner pectoral corners. The upper teeth are of moderate breadth, slightly oblique, notched laterally, and with coarser serrations basally. There is usually no middorsal ridge. A more extreme character is their high vertebral numbers.

The species which most agree with them in overall morphology, including the teeth, and in vertebral characteristics, is the Indo-Pacific *albimarginatus*. On this basis it can be regarded as a member of the group, though it differs trenchantly in its color pattern of white-tipped fins (but *wheeleri* has a white-tipped first dorsal) and also always has a low middorsal ridge.

obscurus-galapagensis group

Features which bind the members of this group together are that they are large sharks, with middorsal ridges that are not

noticeably narrow, with broad or moderately broad upper teeth that are concave laterally and uniformly serrated or at most with slightly coarser serrations basally, bluntly rounded snouts of moderate length, the second dorsal fin origin about over the anal origin, and no obvious color pattern although some fin tips may be dusky. The two central members of the group are *obscurus* and *galapagensis*, both of which are worldwide. Three other species, *plumbeus*, *altimus*, and *perezii* (the first two essentially worldwide, but *perezii* is known only from the Caribbean), also seem referable to the group despite some differences. In *plumbeus* and *altimus* the first dorsal origin is about over the pectoral axil, but although this distinguishes them from the others in which the dorsal fin is relatively farther rearward, it does not appear to be a significant common feature since *plumbeus* and *altimus* differ markedly in other ways. A further distinction of *plumbeus* is that diplospondyly occurs far back, usually behind the pelvic axil. The upper teeth of *altimus*, although broad, are noticeably longer than in the other species, and likewise the snout is longer and the second dorsal origin is further forward relative to the anal. The inclusion of *perezii* in the group is based on its very strong similarity to *galapagensis* in all features except its teeth which are distinctly narrow and strongly notched laterally.

A case could also be made for referring the worldwide *longimanus* to this group, despite its obvious differences in color pattern (white mottled fin tips) and fin size and shape. If these differences are set aside it agrees in most other features, although it is not always ridge backed, it has a shorter snout, and the second dorsal fin is somewhat farther forward relative to the anal. Its difference in color is striking, but it should be noted that its white fin markings are preceded in juveniles by black markings. Its large first dorsal and pectoral fins are less distinctive in their size than in being notably round tipped (particularly the dorsal). Hubbs (1951) suggested that the latter characteristic is "merely the retention of an embryonic feature" and noted that *falciformis* also has a broadly rounded first dorsal. Krefft (1954) proposed that this explanation of neoteny did not mean that the placement of *longimanus* in a separate genus, *Pterolamiops*, is unjustified, since the origin of even much higher taxonomic categories is based on such a persistence of embryonic characters. Although Krefft's proposal has merit, I believe that in the absence of evidence to show that *longimanus* differs from other *Carcharhinus* species in a more fundamental way, it is better treated as a species extreme in some respects but still within the bounds of that genus. If this is accepted, it appears to have most in common with the *obscurus-galapagensis* group.

Other Species and Possible Relationships

falciformis and *sorrah*

Springer (1950) placed the worldwide *falciformis* in *Eulamia*, along with such species as *altimus*, *obscurus*, *perezii*, and *plumbeus*. However, although *falciformis* agrees with them in being a large, ridge-backed shark with pointed pectoral tips, it differs in many other features including particularly the nature of the middorsal ridge and the very low and attenuate second dorsal fin. In these latter features it agrees much more closely with *sorrah*, a species of moderate size from the Indo-Pacific. The middorsal ridge in both of these species is noticeably narrow and very well defined. In both of them also the value for the

relationship between the length of the second dorsal rear tip and second dorsal height is at the extreme for all other *Carcharhinus* species, except *borneensis* (which is obviously different in many other ways). If these similarities are indicative of relationship, it can be noted that they are reinforced by a general similarity of form as well. There are, however, important differences between them also. These include the teeth (upper teeth shape, and also the oblique lower teeth of *sorrah*), the lobe on the anterior nasal flap (virtually absent in *falciformis* but prominent in *sorrah*), the shape of the first dorsal fin, the position at which diplospondyly occurs (unusually rearward in *sorrah*), and the color pattern.

brachyurus

I am unable to align the worldwide *brachyurus* with any other species. Although it comes closest to *limbatus* and *amblyrhynchoides* in being a large, smooth-backed shark with a moderately long and pointed snout, it differs notably from them in other features including particularly the shape of the upper teeth. The latter, which are rather small and somewhat hooked in appearance, are most nearly approached by those of the ridge-backed *perezii*, but I doubt that this similarity is significant. In many aspects of its external morphology *brachyurus* is "average," with morphometric values and fin shapes and positions lying in the midrange of those for all species.

borneensis

This small, smooth-backed, western Pacific species stands apart from all other members of *Carcharhinus* in having a discrete series of enlarged pores along each side of the mouth. In this feature it resembles *Rhizoprionodon*, and this similarity is enhanced by its overall correspondence with species of that genus in external morphology including, in particular, its low attenuate second dorsal whose origin is at least halfway back along the anal base, and its very short pectoral fin. It is further unique amongst *Carcharhinus* species in having diplospondyly occurring slightly in front of the pelvic origin.

CARCHARHINUS SPECIES AND THEIR PRIMARY SYNONYMS

- C. acronotus* (Poey, 1860)
Squalus acronotus Poey, 1860
Carcharias (*Prionodon*) *remotus* Valenciennes in Duméril, 1865
- C. albimarginatus* (Rüppell, 1837)
Carcharias albimarginatus Rüppell, 1837
Eulamia (*Platypodon*) *platyrhynchus* Gilbert, 1892
- C. altimus* (Springer, 1950)
Eulamia altima Springer, 1950
Carcharinus radamae Fourmanoir, 1961
- C. amblyrhynchoides* (Whitley, 1934)
Gillisqualus amblyrhynchoides Whitley, 1934
- C. amblyrhynchos* (Bleeker, 1856)
Carcharias (*Prionodon*) *amblyrhynchos* Bleeker, 1856
Carcharias nesiotes Snyder, 1904
Galeolamna fowleri Whitley, 1944
Galeolamna tufiensis Whitley, 1949
Galeolamna coongoola Whitley, 1964

- C. amboinensis* (Müller and Henle, 1841)
Carcharias (*Prionodon*) *amboinensis* Müller and Henle, 1841
Carcharias (*Prionodon*) *henlei* Bleeker, 1853
Carcharias (*Prionodon*) *brachyrhynchos* Bleeker, 1856
- C. borneensis* (Bleeker, 1858-59)
Carcharias (*Prionodon*) *borneensis* Bleeker, 1858-59
- C. brachyurus* (Günther, 1870)
Carcharias brachyurus Günther, 1870
Carcharias lamiella Jordan and Gilbert, 1883b
Eulamia ahenea Stead, 1938
Carcharinus improvisus Smith, 1952a
- C. brevipinna* (Müller and Henle, 1841)
Carcharias (*Aprion*) *brevipinna* Müller and Henle, 1841
Isogomphodon maculipinnis Poey, 1865
Uranga nasuta Whitley, 1943
Galeolamna fowleri Whitley, 1944 (in part)
Longmania calamaria Whitley, 1944
Carcharinus johnsoni Smith, 1951
Aprionodon caparti Poll, 1951
- C. cautus* (Whitley, 1945)
Galeolamna greyi cauta Whitley, 1945
- C. dussumieri* (Valenciennes in Müller and Henle, 1841)
Carcharias (*Prionodon*) *dussumieri* Valenciennes in Müller and Henle, 1841
Carcharias (*Prionodon*) *tjutjot* Bleeker, 1852
Carcharias (*Prionodon*) *javanicus* Bleeker, 1852
Carcharias malabaricus Day, 1873
- C. falciformis* (Bibron in Müller and Henle, 1841)
Carcharias (*Prionodon*) *falciformis* Bibron in Müller and Henle, 1841
Carcharias (*Prionodon*) *menisorrah* Valenciennes in Müller and Henle, 1841
Squalus tiburo Poey, 1860
Aprionodon sitankaiensis Herre, 1934
Carcharhinus floridanus Bigelow, Schroeder, and Springer, 1943
Eulamia malpeloensis Fowler, 1944
- C. fitzroyensis* (Whitley, 1943)
Galeolamna (*Uranganops*) *fitzroyensis* Whitley, 1943
- C. galapagensis* (Snodgrass and Heller, 1905)
Carcharias galapagensis Snodgrass and Heller, 1905
- C. leucas* (Valenciennes in Müller and Henle, 1841)
Carcharias (*Prionodon*) *leucas* Valenciennes in Müller and Henle, 1841
Carcharias (*Prionodon*) *zambezensis* Peters, 1852
Squalus obtusus Poey, 1861
Squalus platyodon Poey, 1861
Eulamia nicaraguensis Gill and Bransford, 1877
Carcharias azureus Gilbert and Starks, 1904
Carcharias spenceri Ogilby, 1910
Galeolamna (*Bogimba*) *bogimba* Whitley, 1943
Galeolamna greyi mckaili Whitley, 1945
Galeolamna mckaili Whitley, 1951a
Carcharhinus Vanrooyeni Smith, 1958b
Carcharhinus leucas leucas Urist, 1962
Carcharhinus leucas nicaraguensis Urist, 1962
- C. limbatus* (Valenciennes in Müller and Henle, 1841)
Carcharias microps Lowe, 1840
Carcharias (*Prionodon*) *limbatus* Valenciennes in Müller and Henle, 1841
Carcharias (*Prionodon*) *pleurotaenia* Bleeker, 1852
Carcharias (*Prionodon*) *Mülleri* Steindachner, 1867
Carcharias Ehrenbergi Klunzinger, 1871

- Carcharias aethalorus* Jordan and Gilbert, 1883a
Carcharias phorcys Jordan and Evermann, 1904
Carcharhinus natator Meek and Hildebrand, 1923
Galeolamna pleurotaenia tilstoni Whitley, 1950
C. longimanus (Poey, 1861)
Squalus (carcharias) maou Lesson, 1830
Squalus longimanus Poey, 1861
Carcharias insularum Snyder, 1904
Pterolamiops magnipinnis Smith, 1958a
Pterolamiops Budkeri Fourmanoir, 1961
C. melanopterus (Quoy and Gaimard, 1824)
Carcharias melanopterus Quoy and Gaimard, 1824
Carcharhinus commersonii Blainville in Vieillot, 1825
Carcharias (Hypoprion) playfairii Günther, 1870
Carcharias marianensis Engelhardt, 1912
C. obscurus (Lesueur, 1818)
Squalus obscurus Lesueur, 1818
Carcharias (Prionodon) obvelatus Valenciennes in Webb and Berthelot, 1844
Carcharias macrurus Ramsay and Ogilby, 1887a
Galeolamna (Galeolamnoides) eblis Whitley, 1944
Carcharinus Iranzae Fourmanoir, 1961
C. perezii (Poey, 1876)
Platypodon Perezii Poey, 1876
Eulamia springeri Bigelow and Schroeder, 1944
C. plumbeus (Nardo, 1827)
Squalus plumbeus Nardo, 1827
Carcharias (Prionodon) milberti Valenciennes in Müller and Henle, 1841
Carcharias ceruleus De Kay, 1842
Lamna caudata De Kay, 1842
Carcharias (Prionodon) japonicus Temminck and Schlegel, 1850
Carcharias obtusirostris Moreau, 1881
Carcharhinus stevensi Ogilby, 1911
Carcharinus latistomus Fang and Wang, 1932
Galeolamna dorsalis Whitley, 1944
C. porosus (Ranzani, 1840)
Carcharias porosus Ranzani, 1840
Carcharias (Prionodon) Henlei Valenciennes in Müller and Henle, 1841
Carcharhinus cerdale Gilbert in Jordan and Evermann, 1898
C. sealei (Pietschmann, 1913)
Carcharias borneensis Seale, 1910
Carcharias sealei Pietschmann, 1913
Platypodon coatesi Whitley, 1939
C. sorrah (Valenciennes in Müller and Henle, 1841)
Squalus Spallanzani Peron and Lesueur in Lesueur, 1822
Carcharias (Prionodon) sorrah Valenciennes in Müller and Henle, 1841
Carcharias (Prionodon) bleekeri Duméril, 1865
Carcharias taeniatus Hemprich and Ehrenberg, 1899
Galeolamna (Galeolamnoides) isobel Whitley, 1947
C. wheeleri n. sp.

KEY TO THE SPECIES OF *CARCHARHINUS*

This key is based chiefly on external characters, including the teeth, but because these show a great deal of intraspecific variation and overlap between species some identifications will require vertebral counts for confirmation. Wide intraspecific variation also means that some species will key out in two places. As is the case with other groups, familiarity with the species will lead to their identification on subtle features such as, for example, nuances of fin shapes which are very reliable but unfortunately do not lend themselves to treatment in keys. The approach used in this key is very similar to that of Bass et al. (1973) in their treatment of southern African species of *Carcharhinus*; however, any shortcomings are my responsibility.

- 1a. First dorsal fin only slightly tapered towards its apex which is broadly rounded; most fins mottled white (adults) or if black tipped there are also black dorsal saddles on the caudal peduncle (juveniles) (up to 3.00 m; worldwide) *longimanus*
- 1b. First dorsal fin obviously tapered towards its apex which is pointed or sharply rounded; fins not mottled white and if black tipped there are not black dorsal saddles on the caudal peduncle 2
- 2a. Second dorsal fin with a conspicuous black tip but all other fins completely lacking dark markings 3
- 2b. Second dorsal fin plain, white tipped or black tipped but if black tipped there are dark markings on the margins or tips of other fins as well 4
- 3a. First dorsal fin erect; dental formula usually $\frac{13-2-13}{13 \text{ or } 14-1-13 \text{ or } 14}$; large basal serrae on lateral margins of upper teeth are themselves serrated; width of pectoral fin 1.4-1.8 in length of anterior margin of pectoral; width of mouth 6.4-8.3% TL; 54-74 precaudal centra (up to 1.00 m; Indo-Pacific) *dussumieri*
- 3b. First dorsal fin falcate; dental formula usually $\frac{12-2-12}{12-1-12}$; large basal serrae on lateral margins of upper teeth are usually not serrated; width of pectoral fin 1.7-2.0 in length of anterior margin of pectoral; width of mouth 4.2-6.6% TL; 74-85 precaudal centra (up to 0.95 m; Indo-Pacific) *sealei*

- 4a. Caudal fin prominently edged with black along entire trailing margin; first dorsal fin plain or with a white tip but never with dark markings 4
- 4b. Caudal fin not prominently edged with black along entire trailing margin or, if it is, the first dorsal fin also has dark or black markings 6
- 5a. First dorsal fin with distinct white tip and trailing margin (up to 1.72 m; western Indian Ocean) *wheeler*
- 5b. First dorsal fin without distinct white tip and trailing margin (up to 2.54 m; Indo-Pacific) *amblyrhynchus*
- 6a. Interdorsal ridge present 7
- 6b. Interdorsal ridge absent 11
- 7a. First dorsal, pectoral, pelvic, and caudal fins with obvious white tips and trailing margins (up to 2.75 m; Indo-Pacific, eastern Pacific) *albimarginatus*
- 7b. First dorsal, pectoral, pelvic, and caudal fins with dark markings or plain or variously dark and plain 1
- 8a. Second dorsal, pectoral, and lower lobe of caudal fin markedly black tipped; first dorsal fin apex narrowly edged with black; anal fin plain; usually only 12 lateral teeth on each side of upper jaw (up to 1.55 m; Indo-Pacific) *sorran*
- 8b. Fins variously plain or dusky tipped but not black and not marked in the above combination; usually not less than 13 and frequently 14 or more lateral teeth on each side of upper jaw 1
- 9a. First dorsal fin origin in front of or over the pectoral axil or at least nearer to it than to the inner pectoral corner 11
- 9b. First dorsal fin origin slightly in front of or over or behind the inner pectoral corner; if in front it is still nearer to the pectoral corner than to the pectoral axil 1
- 10a. Usually 14 lateral teeth on each side of upper jaw; upper teeth not noticeably long; 82-97 precaudal centra (up to 2.40 m; worldwide) *plumbeus*
- 10b. Usually 15 or more lateral teeth on each side of upper jaw; upper teeth noticeably long; 101-110 precaudal centra (up to 2.82 m; worldwide) *altimus*
- 11a. First dorsal fin origin clearly behind inner pectoral corner (up to 3.30 m; worldwide) *falciformis*
- 11b. First dorsal fin origin over or slightly in front of inner pectoral corner 1
- 12a. Not more than 13 upper lateral teeth and 12 lower lateral teeth on each side of jaw (up to 2.95 m; western Atlantic) *perez*
- 12b. Usually at least 14 upper lateral teeth and 13 lower lateral teeth on each side of jaw 1
- 13a. Upper teeth narrow, their lateral margins deeply concave to notched, their medial margins distinctly concave also (up to 2.92 m; worldwide) *brachyurus*
- 13b. Upper teeth broad, their lateral margins concave but not notched, their medial margins straight or convex rather than concave 1

4a.	Height of second dorsal fin 2.1-3.3% TL and 1.3-1.7 in length of its rear tip; 103-109 precaudal centra (up to 3.00 m; insular, worldwide)	<i>galapagensis</i>
4b.	Height of second dorsal fin 1.5-2.3% TL and 1.6-2.1 in length of its rear tip; 86-97 precaudal centra (up to 3.62 m; worldwide)	<i>obscurus</i>
5a.	Entire trailing margin of caudal fin with a narrow but obvious black edging	16
5b.	Trailing margin of caudal fin not or only partly edged with duskiness or black	17
6a.	First dorsal fin apex with a prominent black blotch (up to 1.80 m; Indo-Pacific, Mediterranean)	<i>melanopterus</i>
6b.	First dorsal fin with a narrow black edging on the anterior margin but apex lacks a black blotch (up to 1.50 m; Indo-Pacific)	<i>cautus</i>
7a.	Upper teeth broad, their lateral margins not notched (Fig. 15 t); distance between inner nostrils usually greater than or equal to preoral length	18
7b.	Upper teeth narrow, or if of moderate breadth their lateral margins are clearly notched; distance between inner nostrils usually less than preoral length	19
8a.	First dorsal fin height more than 3.1 times second dorsal fin height; usually 11 lateral teeth on each side of lower jaw; 89-95 precaudal centra (up to 2.23 m; Indo-Pacific, eastern Atlantic)	<i>amboinensis</i>
8b.	First dorsal fin height equal to or less than 3.1 times second dorsal fin height; usually 12 lateral teeth on each side of lower jaw; 101-123 precaudal centra (up to 3.24 m; worldwide)	<i>leucas</i>
9a.	Most fins with obvious black tips	20
9b.	Most fins plain or only some of them have dusky rather than black tips	22
0a.	First dorsal fin origin over or behind inner pectoral corner; length of anterior margin of pectoral fin usually less than 16% TL; lower teeth usually smooth edged (up to 2.78 m; Indo-Pacific, Atlantic)	<i>brevipinna</i>
0b.	First dorsal fin origin usually over or just behind pectoral axil and always in front of inner pectoral corner; length of anterior margin of pectoral fin usually more than 16% TL; lower teeth serrated	21
1a.	Distance between inner nostrils 1.3-1.7 in preoral length; height of second dorsal fin 1.1-1.6 in length of its rear tip (up to 2.55 m; worldwide)	<i>limbatus</i>
1b.	Distance between inner nostrils 1.0-1.2 in preoral length; height of second dorsal fin 1.0-1.2 in length of its rear tip (up to 1.66 m; Indo-Pacific)	<i>amblyrhynchoides</i>
2a.	Hyomandibular pores forming a discrete series of five to eight enlarged pores alongside each corner of mouth; height of second dorsal fin 2.2 or more in length of its rear tip (up to 1.00 m; Indo-Pacific)	<i>borneensis</i>
2b.	Hyomandibular pores not forming a discrete series of enlarged pores alongside each corner of mouth; height of second dorsal fin 1.9 or less in length of its rear tip	23
3a.	Upper teeth noticeably narrow, their lateral margins concave but not notched; lower teeth usually smooth edged (up to 2.78 m; Indo-Pacific, Atlantic)	<i>brevipinna</i>
3b.	Upper teeth moderately narrow, their lateral margins notched; lower teeth serrated	24

- 24a. Only 11 lateral teeth on each side of lower jaw; snout tip usually with a dusky to black blotch (up to 1.37 m; western Atlantic) *acronotus*
- 24b. Usually not less than 13 lateral teeth on each side of lower jaw; snout tip plain colored
- 25a. Second dorsal fin origin usually over or slightly behind middle of anal base (up to 1.34 m; Indo-Pacific, eastern Pacific, western Atlantic) *porosus*
- 25b. Second dorsal fin origin over or slightly behind anal fin origin
- 26a. Width of pectoral fin 1.9-2.1 in length of anterior margin of pectoral fin; 96-110 precaudal centra (up to 2.92 m; worldwide) *brachyurus*
- 26b. Width of pectoral fin about 1.5 in length of anterior margin of pectoral fin; 58 precaudal centra (up to 1.50 m; Australia) *fitzroyensis*

SPECIES ACCOUNTS

The order in which the species are dealt with is the same as that in the discussion on intrageneric relationships (p. 20) where most of the species were arranged in species groups. Although some significance is implied in the membership of these groups, there is no suggestion that the placing of the groups relative to each other has any meaning in terms of between group relationships.

Carcharhinus limbatus (Valenciennes in Müller and Henle, 1841) Figures 16, 17, 18

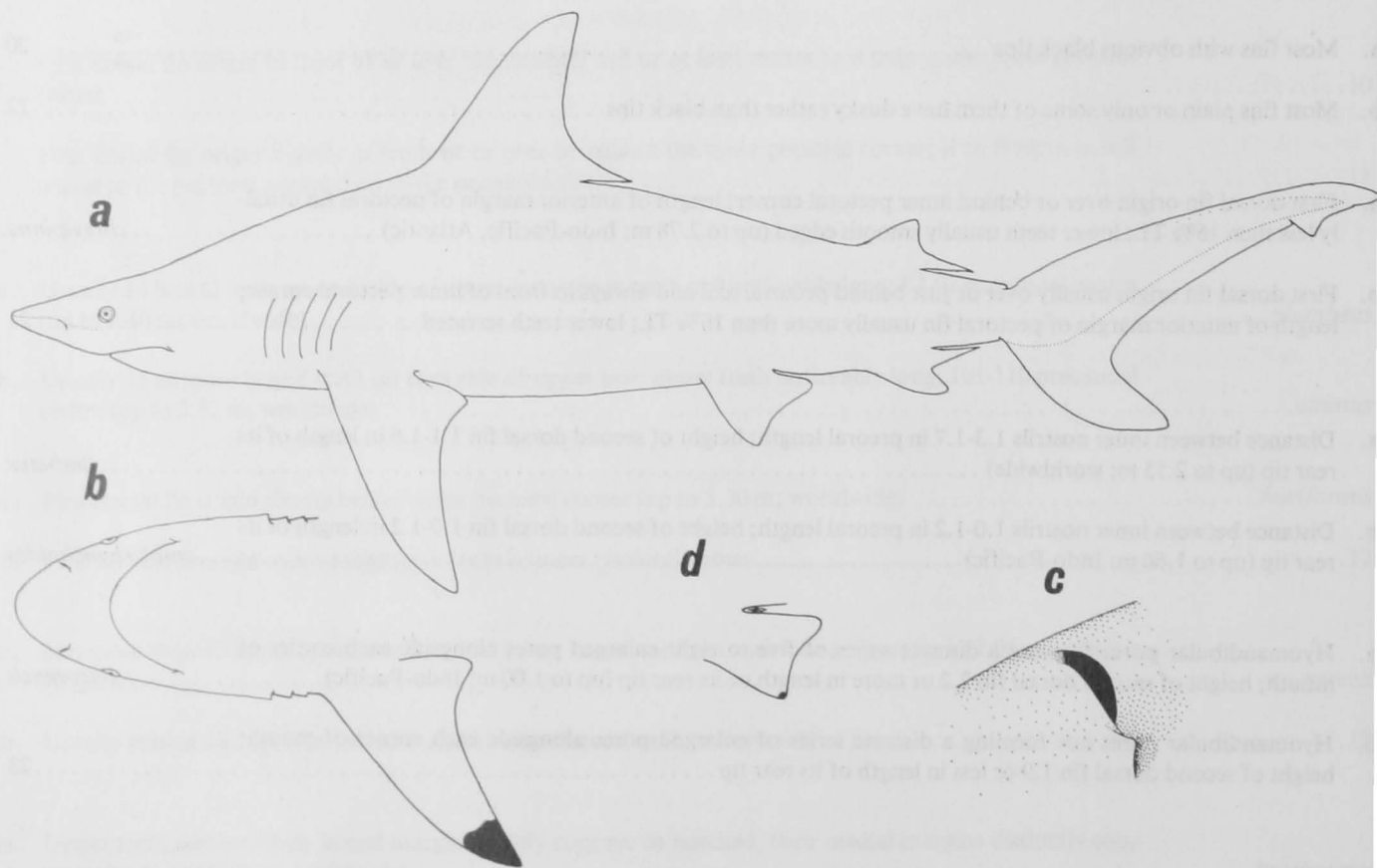


Figure 16.—Atlantic *Carcharhinus limbatus*, USNM 196831, 1,428 mm TL, female from Florida: a, left side; b, underside of head; c, enlarged left nostril; d, underside of right pelvic. Note shape of black mark on pectoral tip in b, and small black mark on pelvic tip in d.

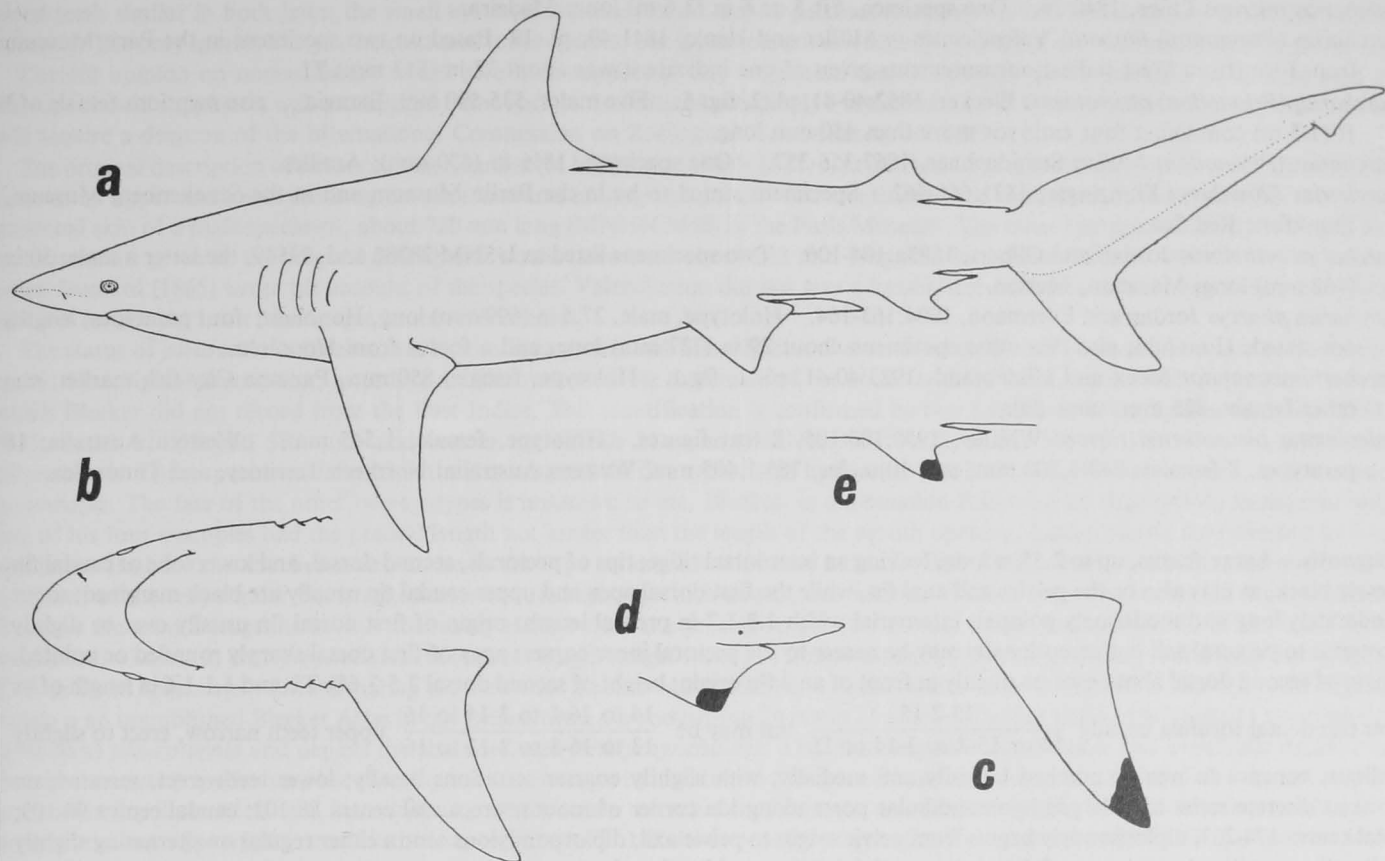


Figure 17.—Pacific *Carcharhinus limbatus*: a, left side of USNM 196598, 1,870 mm TL, male from Hawaii; b, underside of head of same specimen; c, underside of right pectoral of USNM 196790, 1,670 mm TL, male from El Salvador; d, underside of right pelvic of same specimen; e, anal fin of USNM 196822, 1,775 mm TL, male from Guatemala. Note shape of black mark on pectoral tip in c and large black marks on pelvic and anal tips in d and e.

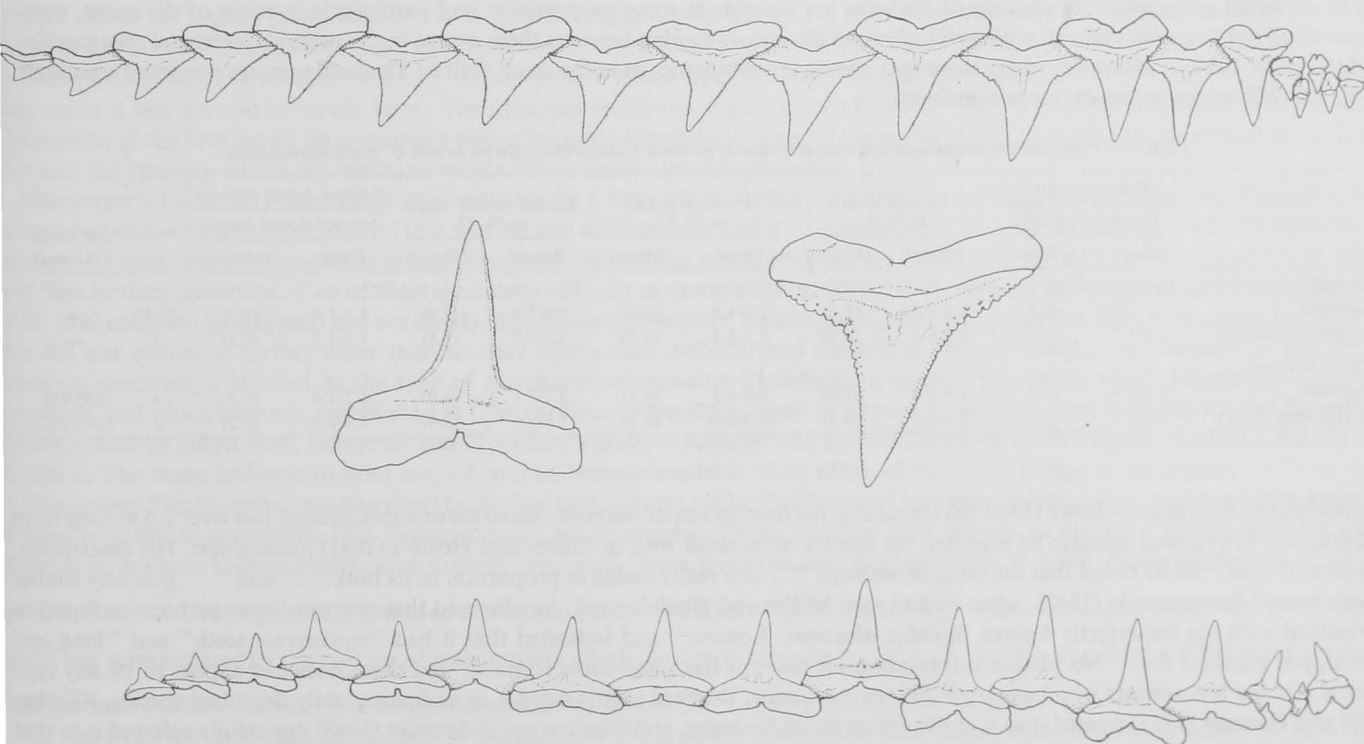


Figure 18.—*Carcharhinus limbatus*, USNM 174074, 1,317 mm TL, female from Australia, Northern Territory: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

Carcharias microps Lowe, 1840:38. One specimen, 8ft 5 or 6 in (2.6 m) long; Madeira.

Carcharias (Prionodon) limbatus Valenciennes in Müller and Henle, 1841:49, pl. 19. Based on two specimens in the Paris Museum from Plée (from West Indies); measurements given of one indicate it was about 32 in (813 mm) TL.

Carcharias (Prionodon) pleurotaenia Bleeker, 1852:40-41, pl. 2, fig. 6. Five males, 535-590 mm, Batavia; also mentions female of 1 ft (1.5 m) containing four embryos more than 450 mm long.

Carcharias (Prionodon) Müller Steindachner, 1867:356-357. One specimen, 18½ in (470 mm); Antilles.

Carcharias Ehrenbergi Klunzinger, 1871:661-662. Specimens stated to be in the Berlin Museum and in the Senckenberg Museum Frankfurt; Red Sea.

Carcharias aethalorus Jordan and Gilbert, 1883a:104-106. Two specimens listed as USNM 28202 and 29549, the latter a male, 30 in (762 mm) long; Mazatlan, Mexico.

Carcharias phorcys Jordan and Evermann, 1904:163-164. Holotype, male, 27.5 in (699 mm) long, Honolulu; four paratypes, length not stated, Honolulu; also two other specimens about 29 in (737 mm) long, and a foetus from Honolulu.

Carcharhinus natator Meek and Hildebrand, 1923:40-41, pl. 1, fig.1. Holotype, female, 850 mm, Panama City fish market; one other female, 825 mm, same data.

Galeolamna pleurotaenia tilstoni Whitley, 1950:100-105, 2 text figures. Holotype, female, 1,545 mm, Western Australia; 10 paratypes, 8 females, 740-1,500 mm, and 10 males, 765-1,405 mm, Western Australia, Northern Territory, and Timor Sea.

Diagnosis.—Large sharks, up to 2.55 m long, lacking an interdorsal ridge; tips of pectorals, second dorsal, and lower lobe of caudal fin clearly black, as may also be the pelvics and anal fin, while the first dorsal apex and upper caudal tip usually are black margined; snout moderately long and moderately pointed; internarial width 1.3-1.7 in preoral length; origin of first dorsal fin usually over or slightly posterior to pectoral axil but exceptionally may be nearer to the pectoral inner corner; apex of first dorsal sharply rounded or pointed; origin of second dorsal about over or slightly in front of anal fin origin; height of second dorsal 2.5-3.6% TL and 1.1-1.6 in length of its rear tip; dental formula usually $\frac{15-2-15}{14 \text{ or } 15-2 \text{ or } 3-14 \text{ or } 15}$ but may be $\frac{14 \text{ to } 16-1 \text{ to } 3-14 \text{ to } 16}{13 \text{ to } 16-1 \text{ to } 3-13 \text{ to } 16}$ upper teeth narrow, erect to slightly oblique, concave to weakly notched laterally and medially, with slightly coarser serrations basally; lower teeth erect, serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 88-102; caudal centra 90-103; total centra 174-203; diplospondyly begins from pelvic origin to pelvic axil; diplospondylous centra either regular or alternating slightly in length; penultimate monospondylous centrum 1.1-1.5 times wider than long.

The circumglobal *limbatus* is remarkably similar to the Indo-western Pacific *amblyrhynchoides*, and to a lesser extent to the worldwide *brevipinna*, with all three of these smooth-backed species sharing common features of a pointed snout, narrow erect upper teeth, and black-tipped fins (particularly the pectorals, second dorsal, and lower lobe of caudal though other fins may be black tipped also). Both *limbatus* and *amblyrhynchoides* differ from *brevipinna* in having the first dorsal origin over or just behind the pectoral axil rather than over or behind the inner pectoral corner as in *brevipinna*. Differences between *limbatus* and *amblyrhynchoides* are mainly in snout proportions and second dorsal fin proportions, *limbatus* being relatively longer snouted and with a lower second dorsal fin. Because different geographic populations of *limbatus* are variable in some proportions, and particularly in those of the snout, comparison of all my *limbatus* material with *amblyrhynchoides* shows overlap between them except in the preoral:internarial relationship, as evidenced in Table 7. However, where these two species are sympatric, as in the small Gulf of Thailand samples presented separately below, the differences are much more trenchant.

Table 7.—Proportional dimensions showing differences between *Carcharhinus limbatus* and *C. amblyrhynchoides*.

	Preoral length Internarial width		Preoral length as % TL		Prenarial length as % TL		Second dorsal height as % TL		Second dorsal rear tip Second dorsal height		n	Size range (TL mm)
	Range	(Mean)	Range	(Mean)	Range	(Mean)	Range	(Mean)	Range	(Mean)		
All localities												
<i>limbatus</i>	1.3-1.7	(1.5)	6.3-9.0	(7.8)	2.7-4.4	(3.8)	2.5-3.6	(2.9)	1.1-1.6	(1.3)	44-57	—
<i>amblyrhynchoides</i>	1.0-1.2	(1.1)	5.3-6.9	(6.2)	2.5-3.1	(2.9)	3.1-3.7	(3.5)	1.0-1.2	(1.1)	7	—
Gulf of Thailand												
<i>limbatus</i>	1.4-1.6	(1.5)	7.6-8.2	(7.9)	3.9-4.3	(4.1)	2.7-3.1	(3.0)	1.2-1.4	(1.3)	4	630-915
<i>amblyrhynchoides</i>	1.0-1.2	(1.1)	5.3-6.6	(5.9)	2.5-2.8	(2.7)	3.4-3.6	(3.5)	1.1-1.2	(1.2)	3	808-1,551

Nomenclatural discussion.—Lowe (1840:38) stated that his description of *microps*, based on one specimen of just over 2.5 m long from Madeira, was provisional because he expected his species to be dealt with in Müller and Henle's (1841) monograph. His description therefore, is brief, but he noted that the teeth of *microps* "...are really feeble in proportion to its bulk..." and "...precisely similar in both jaws." Subsequently (1843), when he had seen Müller and Henle's work, he observed that *microps* "may perhaps be found to be identical with the imperfectly known *Squalus obscurus*, Lesueur" and indicated that it had "equiserrate teeth" and "long and black-tipped pectoral fins." No further information on *microps* has since come to hand, and there does not appear to be any type material. Of the few authors who have used the name *microps*, Duméril (1865) listed it as an inadequately described species, Günther (1870) and Garman (1913) treated it as a junior synonym of *limbatus*, and Bigelow and Schroeder (1948) doubtfully referred it to that species.

Despite the fact that Lowe (1843) himself did not ally his *microps* with *limbatus* even though teeth of the latter were illustrated in Müller and Henle (1841), there is little doubt that his *microps* was *limbatus*. The combination of the large size of the type; the small, ser-

ated teeth similar in both jaws; the small eye; and the long, black-tipped pectoral eliminates other species known from the eastern Atlantic. The only species likely to be confused is *brevipinna*, but it has smooth or virtually smooth lower teeth and a short pectoral fin.

Current opinion on nomenclature would give little support to any suggestion that a name as poorly founded or as little used as *microps* should supplant a well-established name such as *limbatus*. Accordingly I reject *microps* despite its priority, though such action will require a decision of the International Commission on Zoological Nomenclature to validate it.

The original description of *limbatus* Valenciennes (*in* Müller and Henle 1841) is rather brief but taken in conjunction with the illustrations of an upper and lower tooth agrees with *limbatus* as long recognized. The identification is confirmed by the remaining syntype, a mounted skin of a male specimen, about 720 mm long (MNHN 3468) in the Paris Museum. The other syntype, which according to the measurements given in the original description would have been about 843 mm long, has long been lost and was not available even when Duméril (1865) wrote his account of the species. Valenciennes did not give a locality for *limbatus*, but the remaining syntype is labelled as coming from Martinique in the West Indies.

The status of *pleurotaenia* Bleeker, 1852 from Batavia has not been clear, and even Bleeker himself confused two species under this name. His original description, including an illustration of the underside of the snout and the teeth, agrees with *limbatus*, a species which Bleeker did not record from the East Indies. This identification is confirmed by two specimens in the Leiden Museum (RNH 7385, males of 555 and 583 mm) and one in the British Museum (BMNH 1867.11.28, male, 585 mm) labelled as syntypes of *pleurotaenia*. These specimens fall within the size range of the five types listed by Bleeker (1852:40), are of the correct sex, and are clearly *limbatus*. The fate of the other two syntypes is unknown to me. Bleeker, in a discussion following his description, stated that only one of his four examples had the preoral length not longer than the length of the mouth opening. Leaving aside the reference to four specimens (rather than the five stated to be in the type series) this comment indicates that Bleeker had, in addition to *limbatus*, a specimen of the very similar but much shorter snouted species which I recognize here (p. 37) as *amblyrhynchoides*. In my material of *limbatus* the mouth length is always noticeably shorter than the preoral length (the former length averaging 65% of the latter in 45 specimens) whereas in *amblyrhynchoides* the mouth length ranges from just longer to slightly shorter than the preoral length (averaging 77% in seven specimens). Substantiating the view that Bleeker was confusing *limbatus* and *amblyrhynchoides* under the name *pleurotaenia* is an unpublished Bleeker Atlas in the Leiden Museum comprising 24 plates of sharks of which plate 14 is labelled *Cynocephalus* (*Prionace*) *pleurotaenia* and depicts the short-snouted *amblyrhynchoides*. This plate suggests that Bleeker had eventually decided on the short-snouted species as *pleurotaenia*, but this interpretation should not be maintained because the original description and its accompanying illustration and the remaining syntypes are referable to the longer snouted *limbatus*. To avoid further confusion I designate as lectotype of *pleurotaenia* the larger (583 mm TL) of the two male syntypes (both catalogued as RNH 7385) of *pleurotaenia* in the Leiden Museum.

Fowler (1941) described and figured as *pleurotaenia* two specimens from the Philippines and "Indian Archipelago," but these are also the short-snouted *amblyrhynchoides*.

Although Steindachner (1867:356) did not illustrate his *mülleri* (which name should now be corrected to *muelleri*) and I have not found type material, there is little doubt that he was dealing with *limbatus*. His description of the color pattern (all fin tips black except for the pelvic and anal), the pointed snout, the narrow and finely serrated upper and lower teeth with a dental formula of $\frac{31}{31}$, and the second dorsal fin slightly lower than the anal fin and originating in front of it pointed to *limbatus*. Admittedly some of the above features apply also to *brevipinna*, but that species can be discounted in terms of the color pattern, not only in the disposition of black fin tip markings but also because they were already present in the type of *muelleri* despite its small size (470 mm long) which suggests it was either a late embryo or newly born. The principal feature in which *muelleri* differs from typical *limbatus* is in Steindachner's description of the first dorsal fin originating above the inner (posterior) corner of the pectoral fin rather than above or near the axil, but this still lies virtually within the variation which I have encountered in *limbatus*.

Klunzinger's (1871:661) description of *ehrenbergi* as a new species stemmed from his realization that Müller and Henle's (1841) account of *melanopterus* was based on two species, one of them with a short, rounded snout (= *melanopterus* proper), the other with a moderately long, pointed snout. Klunzinger described the latter as *ehrenbergi*, basing his account on Red Sea specimens in the Berlin and Senckenberg Museums. Two of these specimens still exist as mounted skins (ISZZ 4472 collected by Hemprich and Ehrenberg, and SMF 3592 collected by Rüppell) and are clearly identifiable as *limbatus*. Klunzinger himself had noted that they were similar to *limbatus* but did not comment further other than to state baldly that *limbatus* and *ehrenbergi* were different ("verschieden"). The Berlin Museum specimen is labelled as the type of *Carcharias abbreviatus* Ehrenberg, a manuscript species which Klunzinger cites as a synonym, and which later was republished as *Gymnorhinus abbreviatus*, again as a synonym of *ehrenbergi* in Hemprich and Ehrenberg (1899), edited by Hilgendorf. Hemprich and Ehrenberg's account includes very good illustrations of *ehrenbergi* on plate 7, figures 2 a, b, and c. The name *abbreviatus* does not, of course, become available from either of these two citations in synonymy.

The eastern Pacific *aethalorus* described by Jordan and Gilbert (1883a:104) from off Mazatlan, Mexico, has, in recent years, generally been regarded as conspecific with *limbatus*, and I am in agreement with this view even though, as discussed below, there are some differences between eastern Pacific and Atlantic specimens. Data from the only syntype found (USNM 29549) of the two listed are given in Table 8. The original description of *aethalorus* stated "Number of teeth about $\frac{24}{24}$ but such a count is too low for *limbatus* and is not substantiated by the syntype of *aethalorus* in which the dental formula is $\frac{15-2-15}{13-3-13}$ Jordan and Gilbert (1883a) did not mention *limbatus* in their account, and compared *aethalorus* only with "... *Carcharias lamia* (Risso) ..."

Of the five type specimens mentioned by Jordan and Evermann (1904:164) in their description of *phorcys* from the Hawaiian Islands, I have examined three (holotype, USNM 50612; and two paratypes, SU 12715) and find no reason for distinguishing them from *limbatus*. Data from the holotype are given in Table 8. In their description of *phorcys*, Jordan and Evermann did not refer to any other species of *Carcharhinus*, not even to the eastern Pacific *aethalorus* which Jordan (with Gilbert) had previously described and

Table 8.—*Carcharhinus limbatus*, proportional dimensions in percentage of total length.

	♀ 460 mm Virgin Is. St. John USNM 196542	♂ 585 mm ¹ Batavia BMNH 1867 11.28	♂ 600 mm Brazil Vitória SU 52845	♂ 693 mm ¹ Hawaiian Is. Oahu USNM 50612	♂ 787 mm ¹ Mexico Mazatlan USNM 29549	♀ 880 mm ⁴ Panama Mkt. USNM 79310	♀ 990 mm Red Sea Massawa USNM 179127	♀ 1,317 mm Australia Northern Territory USNM 174074	♀ 1,428 mm Florida USNM 196831	♂ 1,775 mm Guatemala Champerí USNM 196822
Snout tip to										
outer nostrils	3.8	4.2	3.7	4.1	4.1	3.7	3.7	3.6	3.2	3.4
eye	7.6	7.1	7.5	7.8	7.6	7.0	7.2	7.0	6.3	6.6
mouth	8.9	7.3	8.0	8.2	8.1	7.6	7.8	7.3	7.0	7.3
1st gill opening	21.1	—	19.7	19.6	20.5	18.6	19.5	18.5	18.7	20.3
3d gill opening	23.6	—	22.2	21.9	22.9	21.6	22.4	21.6	20.4	22.8
5th gill opening	25.8	24.5	24.0	23.7	24.5	23.5	24.2	23.2	23.5	24.6
pectoral origin	25.0	24.3	23.2	22.8	23.7	22.6	23.2	23.2	22.4	24.0
pelvic origin	49.0	49.7	48.3	48.1	48.9	49.1	50.8	49.1	50.4	50.1
1st dorsal origin	31.7	30.3	30.7	29.1	30.4	28.5	30.8	29.5	29.7	29.9
2d dorsal origin	60.4	62.0	62.7	62.8	60.7	62.5	61.5	63.2	61.9	63.1
anal fin origin	61.3	62.0	63.4	61.9	62.0	62.1	62.8	62.2	62.6	62.5
upper caudal origin	71.8	72.3	73.4	73.0	72.4	72.7	72.8	73.5	70.4	74.3
lower caudal origin	70.9	71.9	72.0	72.3	71.8	72.0	71.8	72.8	70.3	73.7
Nostrils										
distance between inner corners	6.2	5.5	5.6	5.3	5.3	5.3	5.3	5.4	5.2	5.8
Mouth										
width	9.0	8.4	7.3	7.9	8.4	8.6	9.1	9.0	9.5	8.8
length	5.0	5.5	5.3	4.8	5.2	5.1	4.5	5.5	4.8	5.2
Labial furrow lengths										
upper	0.8	0.5	0.4	0.6	0.6	0.7	0.5	0.6	0.6	0.6
lower	0.4	0.5	0.4	0.4	0.4	0.5	0.5	0.5	0.5	0.5
Gill opening lengths										
1st	3.9	—	3.7	3.9	3.6	3.4	4.1	4.0	4.4	3.8
3d	4.1	—	3.8	4.5	4.1	4.4	4.7	4.8	4.9	4.7
5th	2.8	—	2.8	3.2	3.2	3.1	3.6	3.6	3.8	3.2
Eye										
horizontal diameter	2.2	1.9	1.9	1.8	1.7	1.4	1.6	1.6	1.3	1.2
1st dorsal fin										
length of base	11.1	10.3	11.3	12.0	11.4	12.8	11.2	11.5	12.1	11.8
length posterior margin	4.1	3.6	3.5	3.5	3.9	3.7	4.0	4.2	4.1	4.0
height	9.2	10.5	8.2	8.9	10.5	9.9	11.5	12.1	12.4	—
2d dorsal fin										
length of base	4.9	3.6	4.2	4.0	4.7	4.2	4.8	4.3	4.4	4.2
length posterior margin	4.2	3.6	3.8	3.8	4.2	3.9	4.1	4.1	4.1	3.8
height	2.6	2.7	2.5	2.5	2.6	2.8	2.9	3.3	3.6	3.5
Anal fin										
length of base	4.1	3.8	4.5	4.5	4.2	4.3	4.5	5.2	5.1	5.0
length posterior margin	3.9	3.4	3.7	3.4	3.9	3.6	3.6	3.7	3.8	3.4
height	3.0	3.2	3.3	3.0	3.0	3.5	3.5	3.4	3.7	3.7
Pectoral fin										
length of base	5.9	5.5	5.5	5.9	6.3	6.3	6.8	6.4	7.0	6.7
length anterior margin	17.6	17.2	17.7	17.2	17.5	17.3	18.8	19.7	19.5	18.3
length distal margin	11.2	12.3	12.0	12.5	11.4	12.2	14.1	16.7	15.4	15.8
greatest width	9.3	8.4	—	—	—	—	9.3	9.6	10.4	9.8
Pelvic fin										
length of base	5.4	4.0	5.0	4.9	5.1	5.3	5.7	5.8	6.2	6.0
length anterior margin	6.3	5.9	5.8	5.9	6.0	5.5	5.6	6.6	6.7	6.2
length distal margin	5.2	5.5	5.5	5.3	5.3	5.2	5.9	6.2	6.3	5.4
length of claspers	—	2.5	2.3	2.2	2.7	—	—	—	—	8.2
Caudal										
length of upper lobe	28.3	28.0	27.7	27.0	27.6	27.5	28.2	27.3	27.5	27.3
length of lower lobe	13.5	12.3	12.2	12.4	13.6	12.2	13.4	13.6	13.7	13.8
Trunk at pectoral origin										
width	12.4	—	12.2	11.5	12.1	11.6	10.6	11.9	12.9	11.7
height	12.8	—	12.5	13.1	11.7	12.0	13.1	12.9	14.0	11.9
Dental formula	—	—	—	15-2-15 14-3-14	15-2-15 13-3-13	15-2-15 13-2-13	15-3-15 14-2-14	15-3-15 14-2-14	—	—
Vertebrae										
precaudal	97	98	100	99	96	98	94	88	—	—
caudal	98	96	98	100	100	101	98	90	—	—
total	195	194	198	199	196	199	192	174	—	—

¹Syntype of *Carcharias (Prionodon) pleurotaenia*.²Holotype of *Carcharias phorcys*.³Syntype of *Carcharias aethalorus*.⁴Holotype of *Carcharhinus natator*.

which I regard as conspecific, but they did state in a later account (1905) which repeated the description of *phorcys* and gave an excellent illustration (pl. 1) of it that the species of the genus were "...very numerous and difficult of separation."

Meek and Hildebrand's (1923:40) original description of *natator* from two specimens from the Panama City fish market appeared in an account of the fishes of Panama in which they also recognized and described *limbatus* (including *aethalorus* as a synonym) as a separate species. In their key to the species (p. 37) they distinguished *natator* in having a shorter and differently shaped snout ("...abruptly narrowed in advance of nostrils..."), a broader mouth, fewer teeth (26 in *natator* versus 29 in *limbatus* in outer row in each jaw) and these less serrated, and in having "...2 broad indefinite, longitudinal, dark stripes..." (obviously referring to the two borders of upper body color which enclose the lateral stripe or tongue of paler color). I have examined the holotype of *natator* (USNM 79310) and am unable to confirm these differences except for the relatively shorter snout (see Table 8 for data on the holotype) which is unusually short for eastern Pacific specimens of *limbatus* but well within the range for specimens from other localities and particularly the Atlantic. The possibility suggests itself, but cannot be proven, that the type of *natator* was an Atlantic specimen even though purchased at the Panama City fish market. The dental formula of *natator* is $\frac{15-2-15}{13-2-13}$ hence virtually identical with that of the type of

aethalorus ($\frac{15-2-15}{13-3-13}$) which Meek and Hildebrand (1923) synonymized, as I do likewise, with *limbatus*.

Whitley's (1950:101) description of the subspecies *Galeolamna pleurotaenia tilstoni* from Australia was based on a holotype and 18 paratypes, but only fragmentary material remains of this type series except for three early stage embryos of about 140 mm TL. I have examined the embryos and the fragmentary material (jaws and skin sample in the Australian Museum) and find that they are referable to either *limbatus* or to *amblyrhynchoides*; a decision as to which of these two species was involved depends, therefore, on Whitley's description. Whitley gave detailed measurements of the holotype and three paratypes, and from these, and in particular the measurements of the preoral length and the internarial distance, *tilstoni* agrees with *limbatus* rather than the shorter snouted *amblyrhynchoides*. Unfortunately Whitley did not measure the vertical height of the second dorsal fin which is relatively lower in *limbatus* than in *amblyrhynchoides*, but measurements taken from his figure of the holotype of *tilstoni* indicate that the fin height is about 1.9% TL, hence, although outside the range of both species, is much nearer to *limbatus* than to *amblyrhynchoides*. On this evidence I synonymize *tilstoni* with *limbatus*. Whitley described his paratypes C and F as lacking the pale lateral stripe along the body, and as having dental formulae of $\frac{13-1-13}{13-1-13}$ and $\frac{14-1-14}{12-1-12}$, respectively, which suggests that species other than *limbatus* were involved; this view is supported by his measurements of paratype C in which the mouth is too wide, and the first dorsal fin base and the upper caudal lobe are too short for *limbatus*.

Acceptance that the species discussed above are synonyms of *limbatus* must take into account the findings that there are differences in populations from different areas. Springer (1950) foreshadowed this in noting that "The Florida-Antillean *C. limbatus* in series comparison with Texas specimens of similar size has a longer snout and extremes from the two localities are quite different in superficial appearance. The available evidence suggests that *natator* is a subspecies of *limbatus* and that its range extends from unknown limits in Pacific tropical American waters along the Atlantic mainland coasts from the Orinoco to the Mississippi where it intergrades with the typical *limbatus*." My data are too few to be conclusive on Springer's findings, although there is some indication that *limbatus* from the western Gulf of Mexico are born at a smaller size and develop serrations on their lower teeth at a smaller size than do specimens from elsewhere in the Atlantic. I find, however, that these differences and others relating to proportions, vertebral numbers, and to color pattern overlap and intergrade to such an extent when viewed on a global basis that it is not possible to describe significantly discrete intraspecific groupings from different localities. Whether such description will ever be possible will require a much more intensive study using large samples, and coupled with investigations of such factors as migratory behavior and population interchange. At the present time the most striking differences that are apparent in regard to the features of proportions and color occur between *limbatus* on the two sides of America. Western Atlantic *limbatus* are, on average, noticeably shorter snouted than their Pacific (and Indian Ocean) counterparts, as evidenced by the data of Table 9.

Table 9.—Prenarial length as percent of total length in *Carcharhinus limbatus* from different oceans.

Ocean	Range	Mean	n
Atlantic	2.7-4.1	3.6	22
Pacific	3.4-4.4	3.9	21
Indo-Australian region, Indian Ocean, and Red Sea	3.4-4.3	4.0	14

Table 10.—Frequency distribution of precaudal and caudal vertebral numbers in *Carcharhinus limbatus* (arrowed ranges with a number in the middle are data from other authors).

Oceans	Precaudal												Caudal																
	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	90	91	92	93	94	95	96	97	98	99	100	101	102	103
Atlantic							1	4	4	2	2			1							1		3	5	1		1		
Central and eastern Pacific									2	1	3	3	2													2	4	4	1
Western Pacific and Indo-Australian region												1					1		1	2		1	1		1				
Western Indian Ocean and Red Sea			2	1	3		1				1	1	2						1					1	2			1	

Differences in color pattern, particularly in the shape of the black tip of the pectoral fin, are detailed in the description on p. 3. Differences in vertebral numbers are most striking for the few specimens I have from the Indo-Australian region and are summarized in Table 10.

Description (see also Table 8).—Moderately large sharks, growing to at least 2.5 m TL. Midline of back smooth, lacking an interdorsal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles close-packed, overlapping, subcircular in outline in small specimens where they have three longitudinal ridges and three posterior marginal teeth, but more nearly rhomboid in larger specimens where they have five to seven ridges and a corresponding number of feebly developed posterior marginal teeth and are more regularly arranged in diagonal rows.

Snout moderately long and moderately pointed in contour. Anterior margin of eye is slightly forward of front of mouth. Nostril oblique, the anterior margin of each with a low, pointed lobe.

Dental formula $\frac{15-2 \text{ or } 3-15}{14-2 \text{ or } 3-14}$ in 24 of 34 specimens counted; $\frac{15-2-15}{15-1 \text{ or } 3-15}$ in 5; $\frac{15-2-15}{13-1 \text{ or } 2-13}$ in 3; and $\frac{14-2-14}{13-2-13}$ and $\frac{16-2-16}{15-1-15}$

the remaining 2. Upper teeth narrow, erect near the center of the mouth but slightly oblique towards the sides, their lateral margins concave to notched, their medial margins weakly concave, but sometimes weakly notched, both margins finely serrated although basal teeth. Lower teeth narrower than upper, erect, with both margins concave and very finely serrated, except in some newborn and juvenile specimens where the margins are smooth edged or virtually so; one to three small symphyseal teeth.

First dorsal fin moderately high, falcate, and noticeably narrow towards the apex which is sharply rounded or pointed; origin of first dorsal usually above the pectoral axil or very slightly behind it, but sometimes farther posterior and exceptionally almost as far back as the inner (posterior) corner of pectoral fin. Second dorsal fin moderately high and long, almost equal to anal fin; length of second dorsal rear tip 1.1-1.6 (mean 1.3) times its height in 44 specimens; origin of second dorsal above or more often slightly anterior to anal fin. Pectoral fin moderately long, slightly falcate, and sharply pointed distally; origin of pectoral fin usually below the fourth gill opening but sometimes below and between the fourth and fifth gill openings; outer corner of pectoral when latter is addressed to trunk so that its anterior margin is horizontal reaches almost or quite to first dorsal axil in small specimens and to as far back as halfway along first dorsal rear tip in large specimens.

Color of the body in life was described by Kato (1964) as "... upper surface from a brownish-gray to a distinct bronze sheen; under sides white; a band of white along the midlevel of the side from the pelvic fin forward to below the 1st dorsal fin." After preservation in alcohol the same general grayish or brownish color remains, including the tongue of white or pale color which extends along the side. In addition, both in life and after preservation, all or most of the fins are black tipped, though there is variation in this feature with age and geography. Usually the black tips are more prominent in small specimens than in adults. The outer tip of the pectoral fin is always black, particularly on the underside. In Atlantic specimens this black mark has a fairly well defined inner border which may be convex or nearly straight but in either case is more or less squarely across the pectoral fin tip, i.e., it extends as far or farther from the tip along the anterior margin of the fin as it does along the distal margin. In Pacific specimens this black mark is oblique, extending farther from the tip along the distal margin than it does along the anterior margin. In specimens from the Indian Ocean, the Red Sea, and the Indo-Australian region, the black mark is usually of the Atlantic type but the Pacific type also occurs as well as intergrades between the two. Apex of second dorsal fin and tip of lower lobe of caudal fin prominently black; apex of first dorsal fin and tip (and sometimes margin) of upper lobe of caudal fin narrowly edged with black; outer tip of pelvic fin with a small black mark (larger and more prominent in Pacific specimens) in half grown and large specimens from all regions, and this is present also in small specimens from the Pacific but usually is lacking in small specimens from other regions; anal fin usually pale-colored in Atlantic specimens of all sizes and in large specimens from other regions but frequently it is black tipped in small specimens from the Pacific and in some that I have seen from the Indo-Australian region and the Red Sea.

Vertebral counts of eight specimens are given in Table 8 and of another 125 specimens in Table 11.

Table 10 gives the frequency distribution of precaudal and caudal numbers for four major regions of the total geographic range of *limbatus*. Although some of the samples are small and there is overlap, the table indicates that the greatest differentiation is in the western Pacific and Indo-Australian region.

Centrum diameter greater than centrum length even in longest monospondylous centra at posterior of abdomen. Diplospondylosis begins above pelvic base, variably from the front to the rear of the base even in specimens from the same region. Diplospondylous centra either regular in length or alternating slightly but regularly. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.65-0.9 (mean 0.77) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.14-1.50 (mean 1.30) in 27 specimens.

The smallest free-living specimen I have seen was 497 mm TL (from Texas), while the largest embryo was 625 mm (from Senegal). My data (see Material examined) suggest that this considerable variation in size of young at birth is largely geographic, with noticeable differences between even such proximate localities as the western Gulf of Mexico (where very small young are characteristic) and Florida (where medium-sized young have been reported). The largest young, larger than my material, have been recorded from Madagascar, but others not greatly smaller are known from such wide-spaced localities as Brazil, South Africa (Natal), and the Pacific. Table 12 summarizes literature accounts of birth size together with information on the number of young per litter.

Male specimens up to 1,080 mm TL that I have examined have been immature, with clasper lengths ranging from 1.7 to 3.1% TL; for larger males 1,615-1,870 mm, were mature with claspers of 7.8-8.4%. Clark and von Schmidt (1965) reported that in their material from Florida, a male 1,260 mm had immature claspers (4.3% TL) but mature testes, another of 1,340 mm was immature (claspers of 4.1%), while five others, 1,350-1,630 mm, were mature with claspers of 6.5-7.6% TL. Sadowsky (1967a) noted that a 1,486 mm male from Brazil was mature, and Bass et al. (1973) stated that males became mature at 1,800 mm in their South African material. Size at first maturity:

Table 11.—Vertebral numbers in 125 specimens of *Carcharhinus limbatus*.

Specimens		Precaudal	Caudal	Total
FSBC VGS 58-216	Florida, Tampa Bay	96	101	197
FSBC VGS 60-38	Florida, Madeira Beach	96	98	194
USNM 179114	Florida, Sarasota	96	—	—
USNM 179115	Florida, Sarasota	95	—	—
USNM 179116	Florida, Sarasota	95	—	—
USNM 125765	Mississippi, Biloxi	98	97	195
USNM 127108	Texas, Bay Chaland	95	99	194
USNM 116446	Texas, Galveston	95	95	190
USNM 116446	Texas, Galveston	94	97	191
UZMK PO688	Mexico, Campeche Bay	98	97	195
10 specimens, Brazil, Sao Paulo ¹		99-102	—	195-203
BMNH 66.4.10.7	Cape Verde Islands	96	98	194
USNM 179720	Liberia, Kru Station	97	98	195
USNM (Uncat.)	South Africa, Durban	99	99	198
USNM (Uncat.)	South Africa, Durban	97	99	196
USNM (Uncat.)	South Africa, Algoa Bay	98	93	191
86 specimens, South Africa, Natal ²		94-102 (mean 98.5)	—	186-201 (mean 195.7)
USNM 198168	Madagascar	99	102	201
GVF 2383	Gulf of Thailand	90	92	182
GVF 2383	Gulf of Thailand	88	94	182
BMNH 1939.3.23.3	Hong Kong	90	94	184
SU 13822	Borneo	89	97	186
UMMZ 177112	Java	90	99	189
USNM 89089	Marquesas	98	100	198
USNM 179571	Marquesas	96	100	196
SU 12715	Hawaiian Islands	100	101	201
SU 12715	Hawaiian Islands	100	101	201
USNM 62462	Hawaiian Islands	99	99	198
UCLA 53157	Galapagos Islands	99	103	202
UCLA 58-29	Mexico, San Blas	97	99	196
SU 11889	Panama	98	101	199
Range (including counts from Table 8)		88-102	90-103	174-203

¹Counts from Sadowsky (1967a).²Counts from Bass et al. (1973).Table 12.—Size at birth and number of young per litter in *Carcharhinus limbatus*.

Total length (mm) of full term or newly born young	No. of young per litter range (mean)	No. of litters	Month(s) when born	Locality	Source
380-ca. 450	3-4 (3.9)	10	June	Texas	Baughman (1942) (as <i>natator</i>)
00-650	3-9 (usu. 5 or 6)	—	—	Venezuela	Cervigon (1966)
525-610	3-8 (5.8)	12	April-June	Florida	Clark and von Schmidt (1965)
540-570	—	—	April	Florida	Springer (1939)
580-660	—	—	—	Pacific	Bigelow and Schroeder (1948)
600-720	3-8 (5.3)	7	December-May	Madagascar	Fourmanoir (1961)
620	1-10 (6.7)	26	November-March	South Africa	Bass et al. (1973)
681	4-9 (6)	—	—	Brazil	Sadowsky (1967a)
685	3-10	—	—	South Africa	D'Aubrey (1964)
—	6	2	January	Florida	Springer (1940)
—	2-7 (5)	3	—	Hawaiian Islands	Tester (see text footnote 4)
—	4	1	—	Western Australia	Whitley (1950) (as <i>tilstoni</i>)

emales usually appears to be about 1,500-1,600 mm TL according to accounts by Bleeker (1852) who gave a figure of 5 ft (ca. 1,500 mm) for a Batavian specimen, Clark and von Schmidt (1965) 1,550 mm for a Florida specimen, and Sadowsky (1967a) 1,580 mm for a Brazilian specimen, but Cervigon (1966) reported that maturity in the female was reached at 1,200 mm for his Venezuelan material. By contrast, Bass et al. (1973) found South African females to be definitely mature only at 1,900 mm. General statements on size at maturity, but not citing sex, were given by Springer (1939) 5 ft (ca. 1,500 mm), Bigelow and Schroeder (1948) about 4-5 ft (ca. 1,200-1,500 mm), and Fourmanoir (1961) 1,700 mm.

The largest male specimen which I examined was 1,870 mm TL, and the largest female 1,805 mm. However, several literature accounts show that *limbatus* grows much larger. Sadowsky (1967a) reported a female of 2,125 mm from Brazil; Bass et al. (1973) recorded males to 2,260 mm and females to 2,470 mm from South Africa; and Tester⁴ listed males and females to 2,550 mm from the Hawaiian Islands.

⁴Tester, A. L. 1969. Cooperative shark research and control program. Final report 1967-69. University of Hawaii, Honolulu, Hawaii. IV + 47 p., 11 figs. Appendix pages A1-A36.

Distribution (see also Material examined).—The fairly extensive range of museum specimens of *limbatus* that I have been able to examine demonstrates that it is a worldwide species, predominantly of tropical seas, but occurring at least seasonally in temperate regions in some areas. Although most specimens and reports of it are from continental coastlines, it is also present at many oceanic islands, and occasional specimens have been taken far offshore. Despite these last-mentioned occurrences *limbatus* does not appear to be a truly oceanic species.

The detailed distribution given below is based mainly on material seen by me, supplemented by reports in Day (1878), Bigelow and Schroeder (1948), Chen (1963—as *melanopterus*), Limbaugh (1963), Cervigon (1966), Kato et al. (1967), Sadowsky (1967a), Guitart-Manday (1968), Bass et al. (1973), and Capapé (1975) which extend its range to other areas. Of the numerous literature reports of *limbatus*, many are mere listings by name only, and these latter, although very likely to be correct, are not included here on that basis alone.

Western Atlantic from southern New England in the north (where *limbatus* is an occasional and seasonal visitor) southwards to southern Brazil, including virtually all eastern United States, the Gulf of Mexico, the Caribbean Sea, with reliably reported occurrences at the Bahamas, Cuba and at several more easterly localities in the West Indies (the syntypes were from Martinique), Venezuela, British Guiana, Surinam, and several localities in Brazil to as far south as Cananéia (lat. 25°S). Eastern Atlantic from Senegal and the Cape Verde Islands and southwards at Liberia, the Gulf of Guinea, and the Belgian Congo. Red Sea and western Indian Ocean where it is known not only from the east African coast to as far south as the tip of South Africa (where it becomes rare) but also from Madagascar, the Seychelles, and other oceanic islands; eastwards it is present around India and the Indo-Australian Archipelago from the Gulf of Thailand southwards through Malaya, the Philippines, Borneo, Java, and New Guinea to Australia (Western Australia, Northern Territory, and Queensland). Pacific Ocean from Hong Kong and China (including the Pescadores) in the northwest, through the Hawaiian Islands, the Marquesas, and Samoa in the central Pacific; and eastward along the Americas from San Diego, Calif., in the north to Ecuador and Peru in the south, and including the Tres Marias, Revillagigedo, Clipperton, and Galapagos Islands.

A record of *limbatus* (as *aethalorus*) from Peru by Hildebrand (1946) included data on 3 embryos from a litter of 23 (which would be remarkably large for *limbatus*); two of these embryos are in the U.S. National Museum and prove to be *brachyurus*.

Tortonese (1938) reported *limbatus* from the Mediterranean on the basis of a specimen from Tripoli, but later (1950) referred the specimen to *maculipinnis* (= *brevipinna*). Ben-Tuvia (1953) listed *limbatus* from Israel (Haifa) and Gohar and Mazhar (1964) tabulated it as a Mediterranean species. More recently Capapé (1975) reported it from the Gulf of Tunis.

Material examined.—AMS IB. 2552, two male and one female embryos, ca. 140 mm (from paratype K of *Galeolamna pleurotaenia tilstoni*), Timor Sea, Evans Shoal, 6 October 1949; BMNH 1961.8.31.4-5, two male embryos, 202 and 207 mm, British Guiana, R. F. McConnell; UZMK PO 694, male embryo, 300 mm, West Indies, Riise; IFAN 56-899, female embryo, 320 mm, Senegal, Gorée, November 1961; IFAN (uncat.), four embryos, two males, 320 and 345 mm, and two females, 355 and 365 mm, Senegal, Gorée, November 1961; IFAN 55-4199, female embryo, 360 mm, Senegal, Gorée, 9 December 1961; IFAN 56-126, male embryo, 400 mm, Senegal, Gorée, 8 April 1956; UZMK PO 688, male embryo, 405 mm, Mexico, Campeche Bay, Laguna de Terminos, 14 February 1911; J. Frederiksen; USNM 196542, female embryo, 460 mm, Virgin Islands, St. John, Lameshur Bay, 1 April 1961, R. Schroeder and Randall; IFAN 56-160, male embryo, 465 mm, Senegal, Joal, 7 May 1956; IFAN 56-145, male embryo, 475 mm, Senegal, Joal, 9 April 1956, J. Cadenat; USNM 197861, male embryo, 485 mm, South Africa, Natal, Durban, 1962; NMV 61-368, female embryo, 490 mm, Surinam, 1865; USNM 116446, three females, 497 to 577 mm, Texas, Galveston, 7 July 1940, J. L. Baughman; USNM 127117, female, 513 mm, Louisiana, Grand Terre, 2 July 1930, I. Ginsburg; IFAN 56-125, male embryo, 515 mm, Senegal, Joal, 8 April 1956, J. Cadenat; USNM 43435, male embryo, 520 mm, Florida, Key West, 1889, J. A. Henshall; DIRU, male embryo, 530 mm, South Africa, Algoa Bay; USNM 125765, female, 535 mm, Mississippi, Biloxi, September 1931, S. Springer; UZMK PO 693, male, 543 mm, West Indies; RNH 7385, two males, 555 and 583 mm [syntypes of *Carcharias (Prionodon) pleurotaenia*], Batavia, Bleeker; BMNH 69.5.14.12-13, two males, 560 and 685 mm, Seychelles, E. P. Wright; UMMZ 177112, female, 573 mm, Java, Batavia, 6-15 May 1921; J. D. F. Hardenberg and C. L. Hubbs; FSBC VGS 60-38, male embryo, 580 mm, Florida, Madeira Beach, 26 April 1960, J. Hurlb Jr.; UCLA 53-157, female embryo, 598 mm, Galapagos Islands, Bartholomew Island, 5 January 1953, B. W. Halstead and Bunker; BMNH 1867.11.28, male, 585 mm [syntype of *Carcharias (Prionodon) pleurotaenia*], Batavia, P. Bleeker; MRAC 71165, male embryo, ca. 590 mm, Belgian Congo, Moanda, August 1947, Darteville; NMV 61-370 and 61-403, two females, 595 and 625 mm, India, Malabar, 1886; ISZZ 4472, mounted skin of female, ca. 600 mm (type of manuscript species *Carcharias abbreviatus*, and syntype of *Carcharias ehrenbergi*), Red Sea, Hemprich and Ehrenberg; SU 52845, male embryo, 600 mm, Brazil, Vitória, 9 December 1944; SU 13822, male, 600 mm, Borneo, Sandakan, 1929, A. W. Herre; USNM 179571, female, 605 mm, Marquesas Islands, Nukunui Hiva, 21 March 1954, Heeny Yuen; USNM 79299, female, 615 mm, Panama Market, 21 April 1911, S. E. Meek and S. F. Hildebrand; IFAN 56-128, female embryo, 615 mm, Senegal, Joal, 10 April 1956, J. Cadenat; RNH 7387, male, 615 mm, Batavia, 1852, P. Bleeker; BMNH 1939.3.23.3, female, 615 mm, Hong Kong, Herklots; NMV 61-356, female, 617 mm, Hong Kong, 1892; SMF 5912, male, ca. 625 mm, Galapagos Islands, 1 October 1962, I. Eibl-Eibesfeldt; IFAN 56-127, male embryo, 625 mm, Senegal, Joal, 10 April 1956, J. Cadenat; GVF 2383, male, 630 mm, and female, 680 mm, Gulf of Thailand, Trat Province, ca. 11°33'N, ca. 102°46'E, 15-20 August 1960; USNM 198168, female, 645 mm, Madagascar, Nossi Bé, 21 March 1964, R. F. Cressy; ANSP 89089, female, 646 mm, Marquesas Islands, Nuku Hiva, 21 March 1937, Vanderbilt South Pacific Expedition; USNM 179720, male, 647 mm, Liberia, Kru Station, 15 October 1952, G. C. Miller; SMF 5778, female, 650 mm, Galapagos Islands, Indefatigable Island, 1960, I. Eibl-Eibesfeldt; IRSN 691, male, 660 mm, Gulf of Guinea, S. of Ile Principe, 24 January 1938, *Mercator*; BMNH 69.5.14.11, female, 660 mm, Seychelles, E. P. Wright; MNHN 97-719, male, 662 mm, Gulf of California, Diguets; UCLA 58-304, male, 663 mm, Panama Bay between Punta Hicacal and Rio Pasiga, 7-9 September 1958; FSBC VGS 58-216, male, 686 mm, Florida, Tampa Bay, 23 August 1958, G. O'Neil; SMF 5222, female, ca. 690 mm, Galapagos Islands, Abingdon Island, 1957, I. Eibl-Eibesfeldt; USNM 50612, male, 693 mm (holotype of *Carcharias phorcys*), Hawaiian Islands, Oahu, Honolulu, 1901, D. S. Jordan and B. W. Evermann; BMNH 66.4.10.7, female, 600 mm, Cape Verde Islands, R.T. Lowe; USNM 62462, male, 710 mm, Hawaiian Islands, Kauai, Hanalei Bay; MNHN 3468, mount-

skin of male, ca. 720 mm [syntype of *Carcharias (Prionodon) limbatus*], Martinique, Plée; USNM 62482, male, 725 mm, Hawaiian Islands, Kauai, Hanalei Bay; USNM 61233, female, ca. 725 mm, Hawaiian Islands, *Albatross*; NMV 61-369, male, 730 mm, China, Post; SU 12715, two males, 731 and 733 mm (paratypes of *Carcharias phorcys*), Hawaiian Islands, Oahu, Honolulu, 1901, D. S. Jordan and B. W. Evermann; USNM 100994, female, ca. 750 mm, Mexico, Guerrero, Zihuantanejo, 17 March 1935, L. A. Walford; NMV 61-392 and 61-451, two females, 765 and 790 mm, Red Sea, Hanfela, 1897; NMV 61-450 and 61-453, male, 765 mm, and female, 840 mm, Red Sea, Shumma Island, Massaua, 1896; USNM 46851, male, ca. 775 mm, Mexico, Baja California, Concepcion Bay, *Albatross*; USNM 29549, male, 787 mm (syntype of *Carcharias aethalorus*), Mexico, Sinaloa, Mazatlan, C. H. Gilbert; SU 11889, female, 790 mm, Panama, 1896, C. H. Gilbert; QMB I.6882, female, ca. 790 mm, Queensland, Salamander Rocks, February 1940, G. Coates; ISZZ 15990, female, 800 mm, Panama, Stanford University; BMNH 1903.5.15.337, male, 845 mm, Pacific Panama, D. S. Jordan; UCLA 60-51, female, 847 mm, Mexico, Baja California, Bahia las Animas, 25-26 January 1960; USNM 127108, female, 850 mm, Texas, Bay Chaland, 2 August 1930, I. Ginsburg; NMV 61-430, female, 850 mm, California, San Diego, January 1874, Steindachner; UCLA 58-29, two males, 861 and 1,053 mm, Mexico, Nayarit, San Blas, 3 February 1958; UCLA 58-46, female, 870 mm, Mexico, Sinaloa, off Isla San Ignacio and Isla Macapule, 10-14 February 1958; USNM 197366, female, 874 mm, Mississippi, off Pascagoula, P. J. Struhsaker; USNM 79310, female, 880 mm (holotype of *Carcharhinus natator*), Panama City Fish Market, 26 January 1911, S. E. Meek and S. F. Hildebrand; GVF 2467, two females, 886 and 915 mm, Gulf of Thailand, Trat Province, ca. 11°56'N to 12°03'N, ca. 102°14'30"E to 102°17'45"E, 12 January 1961; UCLA 58-47, female, 907 mm, Mexico, Sinaloa, south of Bahia Topolobampo, S of Isla San Ignacio and Isla Macapule; SMF 3592, mounted skin of female, ca. 965 mm (syntype of *Carcharias ehrenbergi*), Red Sea, 1828, E. Rüppell; USNM 179127, female, 990 mm, Red Sea, Massawa, 1-6 April 1962, E. Clark; USNM 170487, female, ca. 1,030 mm, Philippine Islands, South Tumindao Island, 26 February 1908, *Albatross*; USNM 197365, male, 1,080 mm, Louisiana, S of Grand Isle, 29°05'N, 89°56'W, 26 September 1961, *Oregon*; AMS IB.3803, jaws of male, 1,230 mm (paratype of *Galeolamna pleurotaenia tilstoni*), Australia, Northern Territory, Jordan Bay, Bathurst Island, 5 September 1949, A. J. Mandell; USNM 174074, female, 1,317 mm, Australia, Northern Territory, Cape Arnhem, 21 August 1948, R. R. Miller; USNM 179116, female, 1,400 mm, Florida, Sarasota, Midnight Pass, 9 June 1963, Cape Haze Marine Laboratory; RNH 2538, mounted skin of female, ca. 1,410 mm, Java, Kuhl and van Hasselt; USNM 196831, female, 1,428 mm, Florida, Dade County, Virginia Key, 8 April 1962, J. Coles, C. D'asaro, and S. Gruber; USNM 196821, female, 1,485 mm, Florida, Dade County, Virginia Key, 8 April 1962, J. Coles, C. D'asaro, and S. Gruber; AMS IB.2421, jaws and skin sample of female, 1,545 mm (holotype of *Galeolamna pleurotaenia tilstoni*), Western Australia, Joseph Buonaparte Gulf, Van Cloon Reef, 15 September 1949, K. Godfrey; USNM 179115, male, 1,600 mm, Florida, Sarasota, Midnight Pass, 9 June 1963, Cape Haze Marine Laboratory; USNM 179112, mature male, 1,615 mm, Florida, Sarasota, 1 mi W of Midnight Pass, 27 May 1963, Cape Haze Marine Laboratory; USNM 196790, mature male, ca. 1,670 mm, El Salvador, 5 February 1962, R. Whitney; USNM 179114, female, 1,770 mm, Florida, Sarasota, Midnight Pass, 6 June 1963, Cape Haze Marine Laboratory; USNM 196822, mature male, 1,775 mm, Guatemala, Champerico, 7 February 1962, R. Whitney and S. Kato; USNM 196830, female, 1,805 mm, Florida, Dade County, Virginia Key, 8 April 1962, J. Coles, C. D'asaro, and S. Gruber; USNM 179113, female, 1,805 mm, Florida, Sarasota, Midnight Pass, 5 June 1963, Cape Haze Marine Laboratory; USNM 196598, mature male, 1,870 mm (discarded except for jaws), Hawaiian Islands, Oahu, Honolulu, August 1961.

Also jaws at several institutions, including SAMC 18219, from Natal, 1931, C. L. Biden; and SMNS 1642½, from Red Sea, Koseir, 1870.

Carcharhinus amblyrhynchoides (Whitley, 1934)

Figures 19, 20

Gillissqualus amblyrhynchoides Whitley, 1934:189-191, text fig. 4. Holotype, female, "nearly two feet long" (610 mm), Australia, Queensland.

Diagnosis.—Moderate-sized sharks, up to 1.66 m long, lacking an interdorsal ridge; tips of pectorals, first and second dorsals, and lower lobe of caudal fin black, and to a lesser extent the pelvics, while the upper caudal is frequently dusky margined; snout short and moderately pointed; internarial width 1.0-1.2 in preoral length; origin of first dorsal over or slightly posterior to pectoral axil; apex of first dorsal sharply rounded or pointed; origin of second dorsal about over or slightly in front of anal fin origin; height of second dorsal 3.1-3.7% TL and 1.0-1.2 in length of its rear tip; dental formula $\frac{15-1 \text{ to } 3-15}{14 \text{ or } 15-1 \text{ to } 3-14 \text{ or } 15}$; upper teeth narrow, erect to slightly

oblique, concave to weakly notched laterally and medially, with slightly coarser serrations basally; lower teeth erect, serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 78-96; caudal centra 90-101; total centra 168-193; diplospondyly begins from one-third along pelvic base to just behind pelvic axil; diplospondylous centra either regular or alternating slightly in length; penultimate monospondylous centrum 1.0-1.4 times wider than long.

This Indo-west Pacific species is very like *limbatus*, and these two, together with *brevipinna*, differ from all other species of *Carcharhinus* in having the following combination of characters: no interdorsal ridge, a pointed snout, noticeably narrow erect upper teeth, and black tips on several fins but always including (except in young *brevipinna*) the pectorals, second dorsal, and lower lobe of caudal. A feature which readily separates *amblyrhynchoides* and *limbatus* from *brevipinna* is that they have the first dorsal origin over or just behind the pectoral axil whereas in *brevipinna* it is over or behind the inner pectoral corner. Compared with *limbatus*, *amblyrhynchoides* differs in being relatively shorter snouted and having a higher second dorsal fin. Details of these differences are given in the account of *limbatus* (p. 30) where it is shown that the firmest criterion is the preoral:internarial ratio which in *amblyrhynchoides* is 1.0-1.2 (mean 1.1) in 7 specimens and in *limbatus* is 1.3-1.7 (mean 1.5) in 57 specimens.

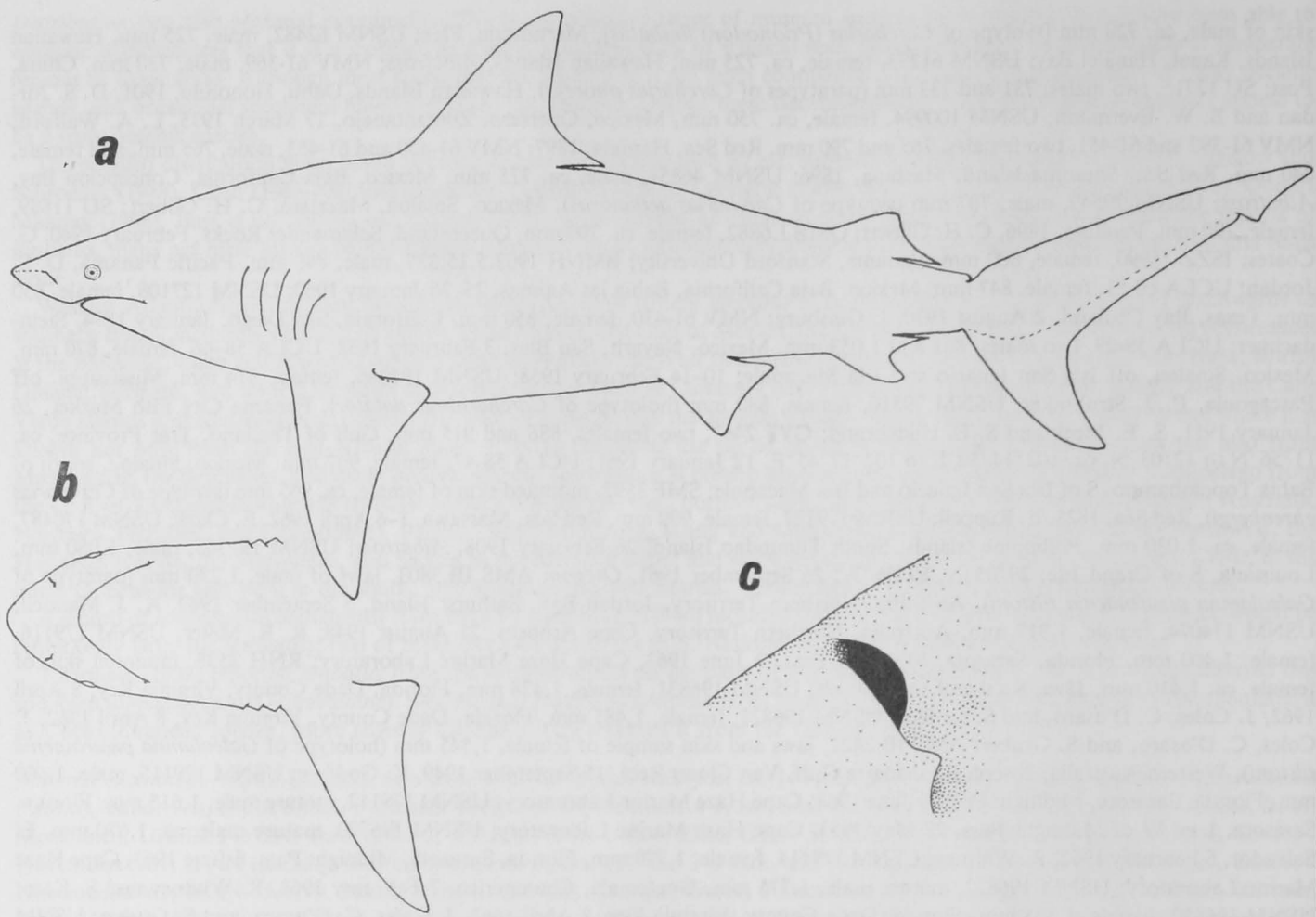


Figure 19.—*Carcharhinus amblyrhynchoides*, GVF 2387, 1,551 mm TL, female from Gulf of Thailand: a, left side; b, underside of head; c, enlarged left nostril.

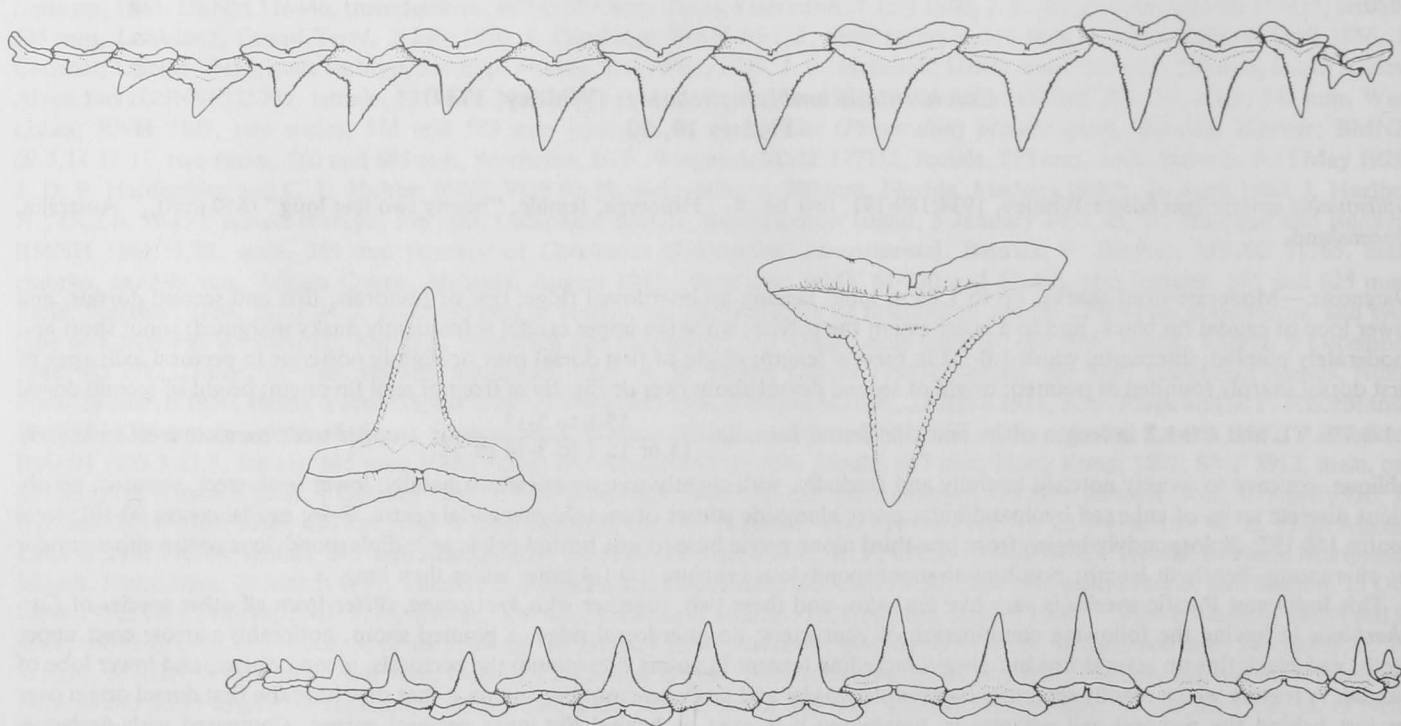


Figure 20.—*Carcharhinus amblyrhynchoides*, USNM 32705, 530 mm TL, female from "Indian Archipelago": right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

Nomenclatural discussion.—This species is very poorly known, probably because of its close similarity to *limbatus*. Bleeker (1852) confused it with *limbatus*, as evidenced by his remarks following his description of *pleurotaenia* (= *limbatus*) from Batavia, and by an unpublished Bleeker plate in the Leiden Museum which is labelled as *pleurotaenia* but is clearly *amblyrhynchoides* (see my Discussion, p. 31). Fowler (1941) similarly described as *pleurotaenia* two specimens of *amblyrhynchoides*, one from the Philippines, the other from the "Indian Archipelago." Whitley's (1934:189) account of a specimen, as a new species *amblyrhynchoides*, from Queensland, Australia, provides, therefore, the oldest valid name for the species. Whitley's specimen had earlier been reported, by name only, as *Carcharhinus amblyrhynchos* Bleeker by Ogilby (1915, 1916), but Whitley rightly indicated that it could not be that species. Whitley gave an excellent description, with illustrations, of his only specimen, but I find that his statement that the dental formula is $\frac{13-13}{11-11}$ is incorrect; I have examined the holotype, and the formula is $\frac{15-2-15}{15-1-15}$. A summary of the original description appeared in Whitley (1940:94), while subsequently Marshall (1964) stated that *amblyrhynchoides* is common in the waters of North Queensland.

The few specimens known of *amblyrhynchoides* show little variation, except that the holotype has a markedly lower number of precaudal centra than the others (see Table 13). In the absence of other evidence, and particularly until more Australian specimens become available, I am not placing weight on this difference as almost comparable variation occurs in the closely related *limbatus* (see p. 34).

Description (see also Table 13).—Moderately large sharks, growing to at least 1.7 m TL. Midline of back between dorsal fins smooth lacking an interdorsal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles close-packed and overlapping except in small specimens where they are almost or just contiguous, subcircular in outline with three longitudinal ridges and three feeble posterior marginal teeth in small specimens, but more nearly rhomboid with five ridges and teeth in larger specimens.

Snout short but moderately pointed in contour. Anterior margin of eye is above or usually slightly anterior to front of mouth. Nostrils oblique, the anterior margin of each with a low, pointed lobe.

Dental formula $\frac{15-1 \text{ to } 3-15}{14-2 \text{ or } 3-14}$ in three of six specimens counted; $\frac{15-2-15}{15-1-15}$ in two; and $\frac{15-3-15}{15-1-14}$ in one. Upper teeth narrow, erect at the center of the mouth but slightly oblique towards the sides, their lateral margins concave to notched, their medial margins weakly concave, both margins finely serrated although the serrations are sometimes larger and slightly irregular basally; one to three small symphyseal teeth. Lower teeth narrower than upper, erect, concave on both margins, and very finely serrated; one to three small symphyseal teeth.

First dorsal fin moderately high and noticeably narrow towards the apex which is sharply rounded or pointed; origin of first dorsal above the pectoral axil or very slightly behind it. Second dorsal fin moderately high and long, almost or quite equal to anal fin; length of second dorsal rear tip 1.0-1.2 (mean 1.1 in seven specimens) times its height; origin of second dorsal above or more often very slightly anterior to anal fin origin. Pectoral fin long, slightly falcate, and sharply pointed distally; origin of pectoral about below the fourth gill opening; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches to or just behind first dorsal axil.

Color after preservation in alcohol is gray or brownish gray above, white or pale below with a band of this lighter color along the midlevel of the side from the pelvic fin forward to below the first dorsal fin. Most of the fins dusky or black tipped, as follows: outer tip of pectoral with a prominent black mark, particularly on the underside where the mark is more or less square across the tip (i.e., the mark extends about as far along the anterior margin as it does along the distal margin); apex of first and second dorsal fins dusky to black; tip of lower lobe of caudal black, and frequently the anterior and terminal margins of the upper lobe have dusky margins; anterior (outer) tip of pelvic with a small dusky mark; anal fin usually pale colored.

Vertebral counts as in Table 13. A count of one other specimen (BMNH 1925.7.20.14-16, Gulf of Aden) was as follows: precaudal 90, caudal 93+, total 183+, giving ranges for all specimens of 78-96 precaudal, 90-101 caudal, and 168-193 total vertebrae.

Centrum diameter greater than centrum length even in longest monospondylous centra at posterior of abdomen. Diplospondylous centra regular or alternating slightly and regularly in length. Diplospondylous usually above pelvic base, variably from the anterior third to the posterior of the base, but behind base, about midway between pelvic axil and rear tip of pelvic fin, in the holotype of *amblyrhynchoides*. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.73-0.97 (mean 0.82) and the

$\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.26-1.86 (mean 1.59) in six specimens.

The smallest, apparently free-living specimen I have seen was 515 mm TL, and the largest embryo was 550 mm. Juvenile males, up to 884 mm long, had clasper lengths of 2.0-2.4% TL. No information is available on size at maturity, or number of embryos per litter, etc. The largest specimen known is a female of 1,665 mm TL.

Distribution (see also Material examined).—The holotype of *amblyrhynchoides* was from Queensland, Australia, while the few other specimens known are mostly from the Indo-Australian region (Batavia, Borneo, "Indian Archipelago," Gulf of Thailand) and eastwards at Cochin China and the Philippine Islands, and westwards at the Gulf of Aden.

Material examined.—NMV (uncat.), four embryos, three males, 252-262 mm, and one female, 257 mm, southern Arabia (Gulf of Aden), Qishn, 1902, W. Hein; BMNH 1925.7.20.14-16, two embryos, male, 425 mm, and female, 435 mm, Gulf of Aden, A. Ehrenreich; MNHN 7802, male, 515 mm, Cochin China, Harmand; USNM 151228, male embryo, 520 mm, Philippine Islands, Manila

Table 13.—*Carcharhinus amblyrhynchoides*, proportional dimensions in percentage of total length.

	♂ 515 mm Cochin China MNHN 7802	♂ 520 mm Philippines Manila Mkt. USNM 151228	♀ 530 mm Indian Archipelago USNM 32705	1♀ 595 mm Australia Queensland QMB I.2003	♂ 808 mm Gulf of Thailand GVF 1548	♂ 884 mm Gulf of Thailand GVF 1548	♀ 1,551 mm Gulf of Thailand GVF 2387
Snout tip to							
outer nostrils	3.3	2.9	3.1	2.9	2.8	2.5	2.8
eye	6.0	6.0	6.6	6.4	6.3	5.6	5.9
mouth	6.2	6.0	6.8	6.9	6.6	5.9	5.3
1st gill opening	—	17.7	17.7	19.0	19.2	17.5	18.8
3d gill opening	—	20.2	20.6	—	21.3	19.7	21.2
5th gill opening	23.6	22.1	22.5	24.7	22.8	21.2	23.9
pectoral origin	23.2	21.0	21.9	22.6	21.5	20.3	21.4
pelvic origin	48.4	46.9	49.2	46.8	47.2	48.1	49.8
1st dorsal origin	30.4	27.9	28.1	29.8	28.7	28.6	29.6
2d dorsal origin	59.9	62.2	58.5	60.0	60.2	59.6	63.0
anal fin origin	60.7	60.8	59.1	59.5	61.3	60.5	63.2
upper caudal origin	72.3	73.0	70.7	71.9	72.4	72.0	74.4
lower caudal origin	71.5	72.1	70.2	71.0	71.6	71.3	73.6
Nostrils							
distance between inner corners	5.8	6.0	5.8	6.2	5.6	5.5	5.4
Mouth							
width	9.7	8.1	9.4	10.3	8.8	9.0	9.3
length	6.3	4.8	5.5	5.6	5.0	4.9	5.4
Labial furrow lengths							
upper	0.8	0.6	0.7	0.5	0.6	0.6	0.5
lower	0.8	0.4	0.5	0.4	0.4	0.3	0.4
Gill opening lengths							
1st	—	3.5	4.3	3.7	3.7	4.3	4.6
3d	4.8	4.0	4.5	4.4	4.1	4.6	5.6
5th	—	2.9	3.4	3.0	2.8	3.3	3.9
Eye							
horizontal diameter	2.0	1.9	1.9	1.8	1.6	1.5	1.2
1st dorsal fin							
length of base	10.5	12.9	12.1	11.8	11.8	11.4	12.0
length posterior margin	4.1	3.3	3.9	3.5	3.8	4.6	3.7
height	10.3	8.6	10.1	—	12.6	10.9	12.0
2d dorsal fin							
length of base	4.4	4.4	5.3	5.0	4.6	5.1	4.9
length posterior margin	4.0	3.7	3.8	3.9	4.0	4.2	4.2
height	3.7	3.1	3.7	3.2	3.5	3.6	3.4
Anal fin							
length of base	5.0	4.8	4.9	5.4	5.1	5.3	5.0
length posterior margin	3.3	3.1	3.4	3.5	3.4	3.7	3.4
height	3.9	3.1	3.5	3.9	3.4	3.7	3.4
Pectoral fin							
length of base	6.0	5.8	5.7	6.7	6.8	7.1	7.2
length anterior margin	18.6	16.3	18.3	—	18.6	18.4	19.7
length distal margin	14.2	11.3	13.2	—	15.1	14.5	17.5
greatest width	9.3	—	—	—	9.9	10.1	10.4
Pelvic fin							
length of base	4.9	5.6	4.5	6.0	5.7	5.6	5.9
length anterior margin	6.4	6.2	6.1	6.0	6.6	6.4	7.1
length distal margin	6.1	5.4	5.8	6.7	5.8	5.9	6.9
length of claspers	2.4	2.1	—	—	2.0	2.4	—
Caudal							
length of upper lobe	29.3	27.1	28.5	28.6	28.2	29.0	27.7
length of lower lobe	13.6	11.8	13.4	—	13.5	13.8	14.9
Trunk at pectoral origin							
width	—	12.1	13.2	12.8	12.8	12.1	14.2
height	—	12.7	13.6	12.6	14.5	14.1	16.1
Dental formula	15-1-15 14-3-14	15-3-15 15-1-14	15-2-15 15-1-15	15-2-15 15-1-15	15-3-15 14-2-14	15-2-15 14-3-14	—
Vertebrae							
precaudal	91	96	94	78	93	92	
caudal	91	95	95	90	95	101	
total	182	191	189	168	188	193	

¹Holotype of *Gillisqualus amblyrhynchoides*.

Fish Market, 21 April 1909, *Albatross*; USNM 32705, female embryo, 530 mm, Indian Archipelago; RNH 17955, male embryo, 5 mm, October 1947, Zool. Lab. Utrecht; RNH 4264, female, ca. 560 mm, Borneo, 1826, C. A. L. H. Schwaner; QMB I.2003, female, 595 mm (holotype of *Gillisqualus amblyrhynchoides*), Australia, Queensland, Cape Bowling Green, June 1914, H. Harris; NMV (uncat.), female, 660 mm, Batavia, 1855; GVF 1548, two males, 808 and 884 mm, Gulf of Thailand, Chon Buri Province, Chon Buri Ba 13°20'N to 13°27'N, 100°45'15"E to 100°57'E, 7-9 December 1957; GVF 2387, two females, 1,551 and 1,665 mm, Gulf of Thailand, Trat Province, Goh Kut, 11°44'N, 102°35'18"E, 10-20 August 1960.

Carcharhinus brevipinna (Müller and Henle, 1841)
Figures 21, 22

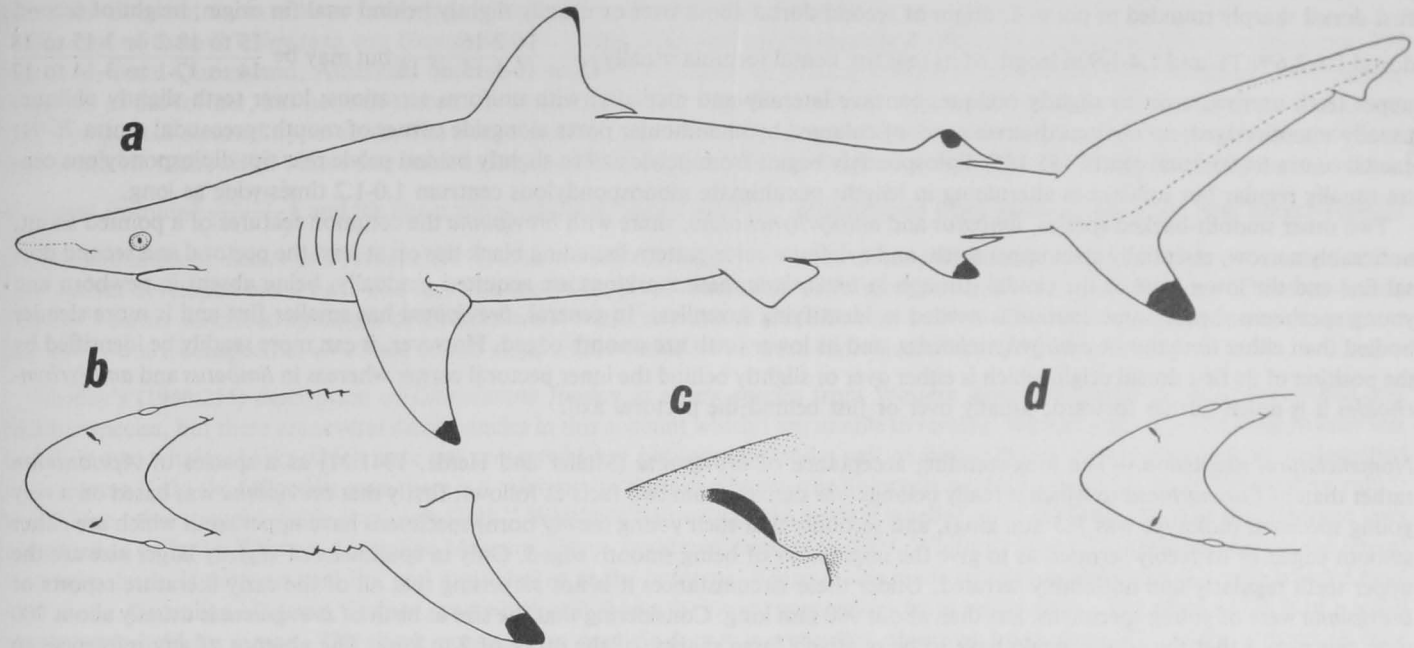


Figure 21.—*Carcharhinus brevipinna*, NMV 2901 (old number), 1,020 mm TL, male from Red Sea; a, left side; b, underside of head; c, enlarged left nostril; d, underside of snout of DIRU (uncat.), 852 mm TL, female from Algoa Bay, South Africa.

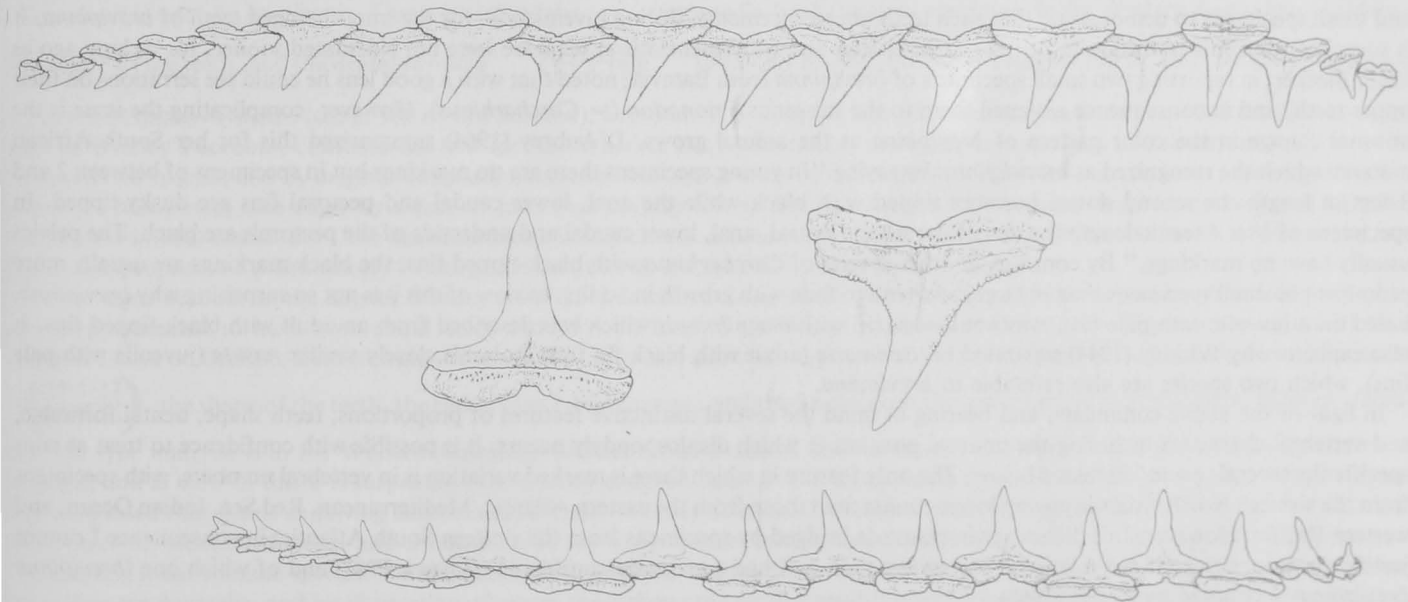


Figure 22.—*Carcharhinus brevipinna*, USNM 109957, from Florida: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

- Carcharias* (Aprion) *brevipinna* Müller and Henle, 1841:31-32, pl. 9. Holotype, 30 in 3 lines (768 mm) long, Java.
- Isogomphodon maculipinnis* Poey, 1865:191-192, pl. 4, figs. 2, 3. Female, 1,715 mm, Cuba.
- Uranga nasuta* Whitley, 1943:115-117, text fig. 1. Female, 727 mm, Queensland, Australia.
- Galeolamna fowleri* Whitley, 1944 (in part):255-256, fig. 2. Holotype, male, about 5½ ft (1,676 mm) long, Western Australia, Exmouth Gulf.
- Longmania calamaria* Whitley, 1944:257-259, text fig. 4. Head and tail of specimen, about 5½ ft (1,676 mm) long, Western Australia, Busselton.
- Carcharinus johnsoni* Smith, 1951:88-92, text figs. 1, 2. Holotype, female, 1,170 mm, South Africa; paratype, female, 875 mm, South Africa.
- Aprionodon caparti* Poll, 1951:41-46, text figs. 16, 17, 18. Holotype, male, 835 mm, Angola; two paratypes, females, 775 and 795 mm, Angola.

Diagnosis.—Large sharks, up to 2.78 m long, lacking an interdorsal ridge; fin tips without dark markings in newborn specimens but becoming increasingly dusky to black with growth so that in subadults the second dorsal, anal, pectorals, and lower lobe of caudal are clearly black tipped, as may also be the first dorsal and upper lobe of caudal and sometimes the pelvics as well; snout long and pointed or sharply rounded; internarial width 1.5-1.8 in preoral length; origin of first dorsal fin over or behind inner pectoral corner; apex of first dorsal sharply rounded to pointed; origin of second dorsal about over or usually slightly behind anal fin origin; height of second dorsal 1.8-2.6% TL and 1.4-1.9 in length of its rear tip; dental formula usually $\frac{16-2-16}{15 \text{ or } 16-1-15 \text{ or } 16}$ but may be $\frac{15 \text{ to } 18-2 \text{ or } 3-15 \text{ to } 1}{14 \text{ to } 17-1 \text{ to } 3-14 \text{ to } 1}$

upper teeth narrow, erect to slightly oblique, concave laterally and medially, with uniform serrations; lower teeth slightly oblique usually smooth edged; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 76-91; caudal centra 84-96; total centra 155-185; diplospondyly begins from pelvic axil to slightly behind pelvic rear tip; diplospondylous centra usually regular but sometimes alternating in length; penultimate monospondylous centrum 1.0-1.2 times wide as long.

Two other smooth-backed species, *limbatus* and *amblyrhynchoides*, share with *brevipinna* the common features of a pointed snout noticeably narrow, essentially erect upper teeth, and a definite color pattern including black tips on at least the pectoral and second dorsal fins and the lower lobe of the caudal (though in *brevipinna* these markings are acquired gradually, being absent in newborn and young specimens, hence some caution is needed in identifying juveniles). In general, *brevipinna* has smaller fins and is more slender bodied than either *limbatus* or *amblyrhynchoides*, and its lower teeth are smooth edged. However, it can more readily be identified by the position of its first dorsal origin which is either over or slightly behind the inner pectoral corner whereas in *limbatus* and *amblyrhynchoides* it is much farther forward, usually over or just behind the pectoral axil.

Nomenclatural discussion.—The long-standing acceptance of *brevipinna* (Müller and Henle, 1841:31) as a species of *Aprionodon* rather than of *Carcharhinus* to which it really belongs was derived from two facts as follows: firstly that *brevipinna* was based on a very young specimen (holotype was 785 mm long), and secondly that such young (newly born) specimens have upper teeth which are either smooth edged or so feebly serrated as to give the impression of being smooth edged. Only in specimens of slightly larger size are the upper teeth regularly and noticeably serrated. Under these circumstances it is not surprising that all of the early literature reports of *brevipinna* were of young specimens, less than about 900 mm long. Considering that the size at birth of *brevipinna* is usually about 70 mm, this means that the adults would have to be relatively large sharks, of the order of 2 m long. The absence of any references to *brevipinna* adults in the early literature suggested either that no adults had been taken, which would be most unusual, or that the adults were masquerading under some other name. In the present study, the examination of a wide size range of specimens confirmed that the latter situation was involved, and that the adult of *brevipinna* had been described as early as 1865 by Poey under the name *maculipinnis*. The serrated upper teeth of *maculipinnis* place it in *Carcharhinus*, but there is an adequate series of intermediate-size and small specimens to demonstrate that such teeth are replacements, during juvenile life, for the smooth-edged teeth of *brevipinna*. It is surprising that this transition in dental characteristics and its nomenclatural sequelae were not elucidated sooner, for as long ago as 1853, Bleeker, in reporting two small specimens of *brevipinna* from Batavia, noted that with a good lens he could see serrations on their upper teeth, and in consequence assigned them to the subgenus *Prionodon* (= *Carcharhinus*). However, complicating the issue is the unusual change in the color pattern of *brevipinna* as the animal grows. D'Aubrey (1964) summarized this for her South African material which she recognized as *maculipinnis* by saying "In young specimens there are no markings but in specimens of between 2 and 3 feet in length the second dorsal becomes tipped with black while the anal, lower caudal and pectoral fins are dusky-tipped. In specimens of over 4 feet in length the tips of the second dorsal, anal, lower caudal and underside of the pectorals are black. The pelvic fins usually have no markings." By contrast, in other species of *Carcharhinus* with black-tipped fins, the black markings are usually more prominent in small specimens than in large, and tend to fade with growth in adults. In view of this it is not so surprising why *brevipinna* based on a juvenile with pale fins, was not associated with *maculipinnis* which was described from an adult with black-tipped fins. It also explains why Whitley (1944) separated his *calamaria* (adult with black fin tips) from his closely similar *nasuta* (juvenile with pale fins), which two species are also referable to *brevipinna*.

In light of the above comments, and bearing in mind the several distinctive features of proportions, teeth shape, dental formulae and vertebral characters including the unusual position at which diplospondyly occurs, it is possible with confidence to treat as conspecific the several species discussed below. The only feature in which there is marked variation is in vertebral numbers, with specimen from the western North Atlantic having lower counts than those from the eastern Atlantic, Mediterranean, Red Sea, Indian Ocean, and western Pacific. However, this difference in counts is bridged by specimens from the western South Atlantic; in consequence I cannot justify the recognition of subspecies of *brevipinna* such as I had previously considered (Garriek 1967) and of which one (*brevipinna brevipinna*) was noted by Krefft (1968).

The holotype of *brevipinna* is a mounted skin (RNH 2525) from Java in the Leiden Museum, and is clearly the specimen described and well illustrated in the original account of the species in Müller and Henle (1841:31, pl. 9). The upper teeth are essentially smooth edged, but on some of them there are rather indistinct serrations towards the bases according to Boeseman⁵ who examined them after removing a coat of varnish with which they had been covered. These incipient serrations could be expected, for in two other comparable-sized specimens that I have seen, of 720 and 757 mm long, the upper teeth were already serrated, whereas in two of 640 mm they were smooth.

Poey's description (1865:191) of *maculipinnis*, supported by his later account (1876) in which he gave additional comment and description, was based on a female specimen of 1,715 mm from Cuba. I do not know if the holotype is still in existence, but the description of it is very good, and the illustrations of the teeth and dermal denticles substantiate it as an adult of *brevipinna* as here recognized.

Whitley (1939:231) recorded from Queensland, Australia, a small, 780 mm, specimen of *brevipinna* in which the upper teeth were still smooth, and in so doing noted that *brevipinna* differed in various proportions from *Aprionodon isodon*, type species of the genus.

⁵M. Boeseman, Curator of Fishes, Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Leiden, Netherlands, pers. commun. October 1963.

Aprionodon. Accordingly, Whitley proposed for *brevipinna* a new genus *Longmania*. Although Whitley was correct in removing *brevipinna* from *Aprionodon*, he did not realize that *brevipinna* was a growth stage of a *Carcharhinus* species, and, judging by his later accounts where he described *brevipinna* specimens under three new specific names and two further generic names, including a new genus, he does not seem to have been clear as to its characterization and status.

The first of these Whitley taxa was *Uranga nasuta*, a new genus and species described (1943:115) from a recently born specimen, 727 mm long, from Queensland, Australia. Several characters supposedly separating *Uranga* from *Longmania* were given in the generic diagnosis of the former, but none of these (first dorsal fin height, second dorsal size relative to anal fin, etc.) can be confirmed except that *Uranga* had serrated upper teeth. The holotype of *U. nasuta* was not preserved, other than for some of the teeth and a sample of skin (AMS IB.1222) which I have examined in the Australian Museum. These fragments, together with Whitley's description of *nasuta*, its dental formula $\begin{pmatrix} 18-16 \\ 16-1-16 \end{pmatrix}$, and his illustration, which he stated was "...reconstructed from measurements and field notes" support the interpretation of *nasuta* as a juvenile *brevipinna* in which the upper teeth had already developed serrations but in which none of the fins had yet developed black tips. The fact that the holotype of *nasuta* had serrated upper teeth at a total length of 727 mm, whereas Whitley's earlier described specimen of *Longmania brevipinna* still had smooth teeth but was 780 mm long, does not negate the view that the two are conspecific, as I have found comparable variation between individuals from other localities.

Whitley's (1944:255) description of *Galeolamna fowleri* as a new species from Western Australia clearly included *brevipinna* plus another species, but there are several discrepancies in this account which I am unable to resolve. Whitley stated (p. 255) that *fowleri* was based on two whaler sharks which were not preserved "but photographs and a pair of jaws indicate that the species is an undescribed *Galeolamna*." On the following page there is a reference to three specimens, the holotype, a "male, about 5½ ft. [1,676 mm] overall," and "Two others caught inside Exmouth Gulf." Whitley's figure 2a of the teeth is labelled as of the holotype, and the holotype jaws are stated to be in the Western Australian Museum, Perth, registered number P. 2503. Whitley's figure 2 is a line drawing of the lateral view of a shark, lacking an anal fin, and also labelled as the holotype. Figure 2 was made by tracing from a photograph which I have seen in the Australian Museum, Sydney, and which still shows the pencil impressions from being traced. The photograph is of a small shark being held by a man. The shark possesses an anal fin but it is somewhat obscured by shadow. The shark appears to be a female—there is no evidence of claspers. Judging by the man's size, the shark could not be longer than about 1,200 mm (4 ft). The shark, therefore, is too small and of the wrong sex to agree with Whitley's published data on the holotype of *fowleri*, yet the traced figure from it is labelled as holotype. This shark is clearly a specimen of *brevipinna* judging by those features shown in this photograph and in another photograph of an oblique underside view of the head region of the same specimen. On this basis *fowleri* must be referred, at least in part, to *brevipinna*. I have examined the jaws, supposedly from the same specimen, in the Western Australian Museum.

The shape of the teeth, and the dental formula $\begin{pmatrix} 13-1-13 \\ 12-3-12 \end{pmatrix}$ definitely are not those of *brevipinna* but instead appear to be from a specimen of *amblyrhynchos* (see p. 106 of this account). Presumably S. Fowler, who obtained the jaws and provided the photographs used in Whitley's account, confused the two species. Whether this is the reason or not, it does not alter the situation that *fowleri* is based on two species, and by original designation has two holotypes—one represented by an illustration made from a photograph of a shark (= *brevipinna*), the other by a pair of jaws (= *amblyrhynchos*). Because the jaws are a more tangible remnant and because Whitley (1944:256) noted that "the dentition alone is sufficiently distinctive, especially as regards the median teeth of lower jaw, to justify the proposal of a new name," I designate the jaws as the operative holotype of *fowleri*.

In the same account as the above, Whitley (1944:257) described *Longmania calamaria* from portions (the head and the tail) of a specimen estimated to have been about 1,650 mm (5½ ft) long, from Western Australia. Despite the fragmentary nature of this material I have no hesitation in referring the account of it to *brevipinna* on the basis of the snout length and shape, the dental formula

$\begin{pmatrix} 17-1-17 \\ 16-1-16 \end{pmatrix}$ the shape of the teeth, the rather long labial furrows, and the black tip on the lower lobe of the caudal fin. Whitley stated that the type material is in the Western Australian Museum, but it cannot now be found. The upper teeth of *calamaria* were finely serrated, and in view of this it is surprising that Whitley assigned *calamaria* to *Longmania* for in two earlier accounts (1939, 1943) he had diagnosed that genus as having smooth-edged teeth. Whitley compared *calamaria* with *brevipinna* and with *nasuta* but the few differences he mentioned (teeth and a black tip to the lower caudal lobe) can be ascribed to the differing ages of the specimens representing these nominal species. Whitley later (1945) reported on a further seven specimens of *calamaria*, 1,000-1,255 mm long, also from Western Australia, and his illustration of one of these shows the black-tipped fins which are a feature of *brevipinna* subadults and adults.

Smith's (1951:88) original description of *johnsoni* from southeastern South Africa is so definitive that, coupled with his excellent illustration of the holotype, leaves no doubt that it is referable to *brevipinna*. The holotype, a skinned-out specimen of 1,170 mm in the Department of Ichthyology, Rhodes University, confirms this identification. Smith (1951) commented that *johnsoni* was very similar to *maculipinnis* but hesitated to regard them as conspecific until actual specimens could be compared. Such differences as he noted between his relatively small specimens and the large female *maculipinnis* described in Bigelow and Schroeder (1948) fall well within the changes in their proportions with growth.

Poll (1951:41) described *caparti* from a small male specimen of 813 mm (IRSN 97) and two small females of 760 mm (IRSN 98) and 785 mm (MRAC 80255) from Angola. I have seen the type specimens and these, together with Poll's excellent description and illustrations, conform to *brevipinna*. Although Poll placed *caparti* in *Aprionodon* he noted that on some of the teeth there were irregularities or sometimes feeble serrations which suggested *Carcharhinus*, hence he commented that *Aprionodon* should have subgeneric rather than generic rank. Poll compared *caparti* with *isodon* and with *brevipinna* but the differences he found in snout length, internarial width, and pectoral length between *caparti* and *brevipinna* are very minor and encompassed within normal variation.

Description (see also Table 14).—Large sharks, growing to at least 2.7 m TL. Midline of back between dorsal fins smooth, lacking an interdorsal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles close-packed, overlapping, subcircular in outline in small specimens, more nearly rhomboid in longer, each with three or more usually five strong longitudinal ridges and corresponding sharp-pointed but short posterior marginal teeth in small specimens, seven or occasionally nine ridges in larger specimens where the marginal teeth are feebly represented.

Snout long and rather pointed in contour though this is variable and some specimens have moderately rounded snouts. Anterior margin of eye above or slightly forward of front of mouth. Nostrils strongly oblique, slitlike, the anterior margin of each with a long pointed lobe.

Dental formula $\frac{16-2-16}{15-1-15}$ in 7 of 26 specimens counted; $\frac{16-2 \text{ or } 3-16}{15 \text{ or } 16-1 \text{ or } 3-15 \text{ or } 16}$ in 6; $\frac{16 \text{ or } 17-2 \text{ or } 3-16 \text{ or } 17}{16 \text{ or } 17-1-16 \text{ or } 17}$ in 8; $\frac{15 \text{ to } 17-2-15 \text{ to } 17}{14 \text{ to } 16-1 \text{ to } 3-14 \text{ to } 16}$ in 4; and $\frac{17-2-18}{17-1-17}$ in 1. Upper teeth narrow, erect near the center of the mouth but slightly oblique laterally

with both margins concave and very finely serrated (except in late embryos and juveniles up to a maximum of about 800 mm long where the upper teeth are smooth initially then show varying degrees of incipient serrations, these usually first appearing near the bases of the cusps); two or three small symphyseal teeth. Lower teeth narrow, slightly oblique except for the most lateral three or four series which are strongly oblique, with both margins concave to almost notched basally, smooth edged in most specimens but showing very feeble and irregular serrations in some adults (particularly females); one to three small symphyseal teeth.

First dorsal fin moderately low, erect rather than falcate, its apex sharply rounded; origin of first dorsal usually above the inner (posterior) corner of the pectoral fin but sometimes behind it by a distance which may be as much as one-half or two-thirds of the length of the posterior (inner) margin of the pectoral fin. Second dorsal fin moderately low and long, almost equal to anal fin; length of second dorsal rear tip 1.4-1.9 (mean 1.6) times its height in 19 specimens; origin of second dorsal slightly posterior to anal fin origin. Pectoral fin moderately short, slightly falcate, and pointed distally; origin of pectoral fin usually below the fourth gill opening but sometimes below and between the fourth and fifth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches only from halfway to two-thirds along first dorsal base in small specimens and only slightly farther back (exceptionally to first dorsal axil) in larger specimens.

Color in life was described by Fourmanoir (1961) as "... gris-violet, la nuance violette s'accroissant sous un fort éclairage solaire. After preservation in alcohol the back and sides are gray while the underside is white or pale; usually a tongue of the paler color extends forward along the side from the pelvic region to below the first dorsal fin, but this is not always obvious. In late embryos and newborn specimens the fins are either pale colored or have only narrow dusky margins, the latter particularly on the upper lobe of the caudal fin and on the apices of the first and second dorsal fins. In slightly larger specimens these dusky marks become black and more extensive (except on the upper lobe of the caudal), and appear also on the lower lobe of the caudal fin, the apex of the anal fin, and the tip of the pectoral fin. In specimens of about 1,000 mm long, or sometimes smaller, the first and second dorsal fins, the anal fin, the pectoral, and the lower lobe of the caudal are prominently black tipped, while the upper lobe of the caudal retains a narrow dusky black edging near its tip. The outer tip of the pelvic fin usually remains pale, but in a few specimens from as widely separated localities as Florida, Angola, the Red Sea, South Africa, and Australia it is dusky or black.

Vertebral counts of five specimens are given in Table 14 and of another 127 specimens in Table 15.

Table 16 gives the frequency distribution of precaudal and caudal numbers for five regions of the geographical range of *brevipinna* and indicates, despite the small size of some of the samples, the marked difference between specimens from the western North Atlantic and those from the eastern Atlantic, Mediterranean and Red Sea, Indian Ocean, and western Pacific Ocean. However, counts for specimens from southern Brazil are intermediate.

Centrum diameter considerably greater than centrum length except in longest monospondylous centra at posterior of abdomen which are almost or quite as long as wide. Diplospondylous centra regular in most specimens, but in some there are a few centra alternating in length along the caudal peduncle. Diplospondyly usually at or slightly behind the pelvic tip but occasionally as far forward

as the pelvic axil. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.86-1.04 (mean 0.94) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.29-1.46 (mean 1.36) in 17 specimens.

The smallest, apparently free-living specimen I have seen was 580 mm TL, while the largest embryo was 790 mm. Comparable larval variation in size at birth was suggested by Springer (1960) whose data in graphical form indicate a range from about 585 to 710 mm for western North Atlantic specimens. Similarly D'Aubrey (1964) reported newborn young at 600-785 mm from South Africa, while Bass et al. (1973), using a larger sample from the same area, noted that birth size is usually from 650 to 750 mm but can be as small as 400 mm or as large as 800 mm. I have seen only juvenile males, up to 1,198 mm long, in which the clasper lengths ranged from 1.3 to 2.2% TL. Sadowsky (1967a) noted that males of 1,592-1,640 mm from Brazil were mature with claspers up to 8% of "Körperlänge," and Clark and von Schmidt (1965) reported six mature males 1,880-2,030 mm from Florida with claspers averaging 7.3% TL. Bass et al. (1973) found that southern African males mature between 1,760 and 2,000 mm. Available data on maturity in the female and number of embryos per litter are tabulated in Table 17.

Sadowsky (1967a) noted that mating occurred from November to January, but predominantly in November, in the material he observed in southern Brazil. Bass et al. (1973) reported that in southern Africa "... young are usually born in April/May after a gestation period of some 12 to 15 months."

The largest specimen of either sex which I have seen was a female of 1,858 mm, but *brevipinna* grows much larger than this. Data from Springer (1960) indicate that males from the northwestern Atlantic grow to about 2,275 mm and females to about 2,400 mm; these sizes are in accord with reports from several other authors. However, occasional specimens may grow larger, e.g., a female of 2,780 mm taken during the Mauritius-Seychelles Fisheries Survey and identified as *sorrah* by Wheeler (1953) but which from his illustration

Table 14.—*Carcharhinus brevipinna*, proportional dimensions in percentage of total length.

	♂ 598 mm	♀ 672 mm	♂ 740 mm	♂ 750 mm						
	Louisiana	Brazil	Western	South						
	USNM	Rio de	Australia	Africa	♂ 813 mm	♂ 865 mm	♂ 1,020 mm		♀ 1,290 mm	♀ 1,858 mm
	127111	Janeiro	BMNH 1927.	Natal	Angola	Florida	Red Sea	♂ 1,198 mm	Red Sea	South Africa
		NMVF 61-394	10.28.1-5	ORID 686	IRSN 97	USNM	NMV 2901	Sumatra	NMV 2492	Natal
						179109	(old no.)	NMVF 61-429	(old no.)	ORID 59
Snout tip to										
outer nostrils	4.7	4.6	4.7	4.5	4.5	4.6	4.5	4.6	4.6	4.3
eye	8.4	8.2	8.2	7.8	8.4	8.4	8.3	—	8.2	7.7
mouth	8.3	8.0	8.6	7.8	8.6	9.0	8.6	8.0	8.5	7.7
1st gill opening	18.9	19.8	20.5	20.3	20.0	20.2	20.2	19.4	21.5	19.6
3d gill opening	21.6	22.4	22.8	22.3	22.5	22.8	22.6	21.7	24.4	22.7
5th gill opening	23.4	24.7	24.7	23.6	24.1	24.5	24.2	24.3	25.6	24.7
pectoral origin	22.7	24.2	24.0	22.9	23.4	24.3	23.4	23.8	24.8	23.9
pelvic origin	49.3	51.2	49.9	49.7	50.5	50.8	50.1	50.5	51.8	51.7
1st dorsal origin	32.8	33.3	33.3	32.0	32.6	33.9	32.7	33.4	33.0	31.9
2d dorsal origin	63.6	62.9	63.1	63.6	63.1	64.1	63.9	63.8	65.0	65.1
anal fin origin	62.5	62.2	62.3	63.2	62.5	63.6	62.9	63.8	64.2	63.5
upper caudal origin	73.7	73.4	73.1	73.7	73.8	74.2	74.6	73.6	75.3	74.8
lower caudal origin	73.1	72.6	72.3	73.6	73.1	73.6	74.1	72.6	74.4	73.9
Nostrils										
distance between inner corners	5.2	5.2	5.0	4.8	5.3	5.2	5.2	4.7	4.9	4.5
Mouth										
width	6.7	7.3	6.4	6.4	8.1	7.9	7.6	7.2	7.6	6.7
length	4.8	4.8	4.5	4.7	4.9	4.5	4.4	4.5	4.6	4.0
Labial furrow lengths										
upper	0.7	0.7	0.7	0.9	0.8	0.8	0.9	0.8	0.8	0.8
lower	0.3	0.7	0.7	0.7	0.6	0.7	0.8	0.9	0.9	0.7
Gill opening lengths										
1st	3.3	4.3	3.2	3.7	3.3	4.0	3.3	4.2	3.6	3.8
3d	4.2	4.3	3.8	5.5	4.1	4.5	3.7	4.2	3.6	4.4
5th	3.3	3.3	2.7	3.7	3.2	3.8	2.9	3.2	2.8	3.2
Eye										
horizontal diameter	2.0	1.7	1.8	1.7	1.7	1.7	1.4	1.4	1.5	1.1
1st dorsal fin										
length of base	9.4	9.2	9.2	9.2	8.8	8.5	9.0	8.9	9.8	10.5
length posterior margin	2.3	3.0	2.7	2.8	2.9	2.8	2.8	3.0	2.6	2.4
height	6.1	7.7	6.0	6.5	8.3	7.4	8.1	8.6	8.8	8.5
2d dorsal fin										
length of base	3.5	3.7	3.5	3.5	3.9	3.4	3.4	3.3	3.3	3.3
length posterior margin	3.2	3.6	3.1	3.6	3.4	3.5	3.4	3.8	3.3	3.6
height	1.9	2.5	1.8	1.9	2.3	2.2	2.2	2.3	2.2	2.2
Anal fin										
length of base	4.5	4.2	4.5	4.3	4.9	4.2	4.3	3.4	4.2	4.5
length posterior margin	3.0	3.3	3.0	3.5	3.1	3.2	3.2	3.7	3.1	3.5
height	2.7	3.2	2.6	2.5	3.1	2.7	2.9	2.9	2.7	2.9
Pectoral fin										
length of base	4.9	5.4	4.9	5.1	5.8	5.2	5.5	5.0	6.0	5.9
length anterior margin	13.7	14.6	13.4	13.6	15.1	14.6	14.9	14.4	15.4	16.0
length distal margin	7.9	11.1	8.4	7.7	11.9	10.7	11.6	11.5	12.4	12.0
greatest width	—	7.9	7.0	7.3	8.2	—	8.1	8.0	8.4	8.1
Pelvic fin										
length of base	4.8	4.1	4.5	4.9	4.8	4.8	4.7	5.0	5.0	4.8
length anterior margin	5.4	4.6	4.1	5.1	4.5	5.2	4.7	4.6	4.7	5.3
length distal margin	3.8	4.6	3.9	3.9	4.7	4.4	4.6	4.8	4.6	4.3
length of claspers	1.8	—	1.6	1.3	1.8	1.7	1.9	1.8	—	—
Caudal										
length of upper lobe	26.1	27.1	25.7	25.7	26.8	25.8	26.6	26.4	25.5	25.6
length of lower lobe	10.2	11.3	10.4	12.1	11.1	11.4	11.6	11.8	12.2	11.9
Trunk at pectoral origin										
width	9.2	10.3	10.0	9.3	10.2	10.3	9.8	—	9.8	11.0
height	9.9	9.8	11.2	10.7	11.7	10.6	10.1	—	10.5	—
Dental formula	16-3-16 15-3-15	16-2-16 15-1-15	17-2-17 17-1-17	16-2-16 16-1-16	16-2-16 15-1-15	16-2-16 15-1-15	16-2-16 15-1-15	17-3-17 16-1-17	—	16-2-17 16-1-16
Vertebrae										
precaudal	78	—	85	—	84	77	—	—	—	86
caudal	86	—	94	—	90	84	—	—	—	93+
total	164	—	179	—	174	161	—	—	—	179+

¹Holotype of *Aprionodon caparti*.

Table 15.—Vertebral numbers in 127 specimens of *Carcharhinus brevipinna*.

Specimens		Precaudal	Caudal	Total
USNM 179111	Florida	76	84	160
USNM 127111	Louisiana	78	86	164
USNM 127133	Louisiana	78	86	164
USNM 127132	Louisiana	79	88	167
	10 specimens, southern Brazil ¹	81-83 (mean 82)	—	155-178 (mean 170)
	southern Brazil ¹	81	87	168
	southern Brazil ¹	82	85	167
	southern Brazil ¹	82	88	170
	southern Brazil ¹	79	87	166
	southern Brazil ¹	81	89	170
	southern Brazil ¹	79	86	165
	southern Brazil ¹	79	85	164
	southern Brazil ¹	78	88	166
	Cape Verde Islands ²	86	91	177
ISZZ 14237	Togo	86	90	176
	Angola ³	85	92	177
	Angola ³	85	92	177
IRSN 98	Angola ⁴	86	88	174
	Israel, Haifa Bay ⁵	87	93	180
	Tunisia ⁶	85	94	179
NMV (uncat.)	Red Sea	86	95	181
ORID 696	South Africa, Natal ⁷	85	62 +	147 +
BMNH 1922.1.13.1.	South Africa, Natal	86	95	181
DIRU (Uncat.)	South Africa, Natal	87	93	180
	89 specimens, the east coast of southern Africa ⁸	83-91 (mean 86.7)	—	174-185 (mean 179.6)
BMNH 1867.11.28.192.	presumably East Indies ⁹	84	90	174
QMB 1.6714	Australia, Queensland	87	94	181
BMNH 1905.10 ...	Japan	88	96	184
USNM 197428	Indian or Pacific Oceans	85	95	180
USNM 197432	Indian or Pacific Oceans	86	94	180
Range (including counts from Table 14)		76-91	84-96	155-185

¹Counts from Sadowsky (1967a).²Counts supplied by V. Sadowsky, Chief Oceanographer, Instituto Oceanografico, Universidade de São Paulo, Canandia, Brazil, pers. commun. March 1970.³Counts from Krefft (1968).⁴Paratype of *Aprionodon caparti*.⁵Counts supplied by A. Ben-Tuvia, Biologist, Marine Resources Section, Fisheries Biology Branch, Food and Agriculture Organization of the United Nations, Via delle Terme di Caracalla, Rome, pers. commun. November 1964.⁶Counts from Quignard and Capape (1971b).⁷Counts supplied by J. D. D'Aubrey, Assistant Research Officer, Oceanographic Research Institute, P.O. Box 736, Durban, South Africa, pers. commun. July 1963.⁸Counts from Bass et al. (1973).⁹Specimen from Bleeker.Table 16.—Frequency distribution of precaudal and caudal vertebral numbers in *Carcharhinus brevipinna* (arrowed ranges with a number in the middle are data from other authors).

Oceans	Precaudal																	Caudal											
	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	84	85	86	87	88	89	90	91	92	93	94	95	
Western North Atlantic	1	1	3	1													2		3		1								
Western South Atlantic				1	3														2	1	2	3							
	← 10 →																												
Eastern Atlantic									1	2	3										1		2	1	2				
Mediterranean and Red Sea										1	1	1														1	1	1	
Indian Ocean and Western Pacific									1	2	2	2	1									1				1	2	1	
	← 89 →																												

tion is *brevipinna*. The largest specimens recorded by Bass et al. (1973) in their large sample from southern Africa were a male of 2,311 mm and a female of 2,660 mm.

Distribution (see also Material examined).—*Carcharhinus brevipinna* has a wide distribution in the Atlantic, Mediterranean, Red Sea, Indian Ocean, and western Pacific, but within these oceans the number of localities from which specimens are known is relatively small. Most of them are coastal, and most lie within the tropics, although in South Africa and western Australia *brevipinna* occurs to about lat. 34°S, and it is also present in comparable latitudes in the Mediterranean and in the western Pacific at Japan. Detailed locality

Table 17.—Size at maturity in the female, and number of young per litter in *Carcharhinus brevipinna*.

Total length of female (mm)	No. of embryos	No. of litters	Locality	Source
1,702-2,213	2-14 (mean 6)	—	Brazil	Sadowsky (1967a, as <i>maculipinnis</i>)
1,875	10	1	Florida?	Bigelow and Schroeder (1948, as <i>maculipinnis</i>)
1,890	6	1	Brazil	Sadowsky ¹
2,100	6	1	Mauritius-Seychelles	Wheeler (1953, as <i>sorrah</i>)
2,120-2,660	6-15 (mean 10.7)	10	South Africa	Bass et al. (1973, as <i>brevipinna</i>)
2,160	3	1	Red Sea	Gohar and Mazhar (1964, as <i>maculipinnis</i>)
2,780	11	1	Mauritius-Seychelles	Wheeler (1953, as <i>sorrah</i>)

¹V. Sadowsky, Chief Oceanographer, Instituto Oceanografico, Universidade de São Paulo, Cananéia, Brazil, pers. commun. March 1970.

given below are based principally on material that I have seen supplemented by literature reports [as *maculipinnis* for most localities by Poey (1865), Tortonese (1950), Springer (1960), Lowe (McConnell) (1962), Sadowsky (1967a), Quignard and Capapé (1971b), and Capapé (1975); as *sorrah* by Wheeler (1953); as *johnsoni* by Fourmanoir (1961); as *calamaria* by Whitley (1968); and as *brevipinna* by Ben-Tuvia (1966), Krefft (1968), and Bass et al. (1973)].

Western Atlantic from the Bahamas, Florida, Mississippi, Louisiana, and Cuba in the north, and from British Guiana and Brazil (Vitória, Rio de Janeiro, and Cananéia) in the south; eastern Atlantic at Cape Verde Islands, Senegal, Togo, and Angola; southern Mediterranean at Tunisia, Libya (Tripoli), and Israel (Haifa Bay); Red Sea; western Indian Ocean at the Mauritius-Seychelles area, Madagascar, Europa Island, and on the east coast of Africa from southern Mozambique to southern South Africa (Mossel Bay); Indo-Australian region at Java, Sumatra, and at Western Australia, Queensland, and New South Wales; western Pacific at Japan.

Literature listings by name only, as *brevipinna*, also include Oman and Muscat in the Arabian Sea, and the Philippine Islands; these are probably correct but there are no further data or specimens to substantiate them.

Ben-Tuvia (1966) regarded Mediterranean specimens of *brevipinna* as being of recent Red Sea origin, as immigrants through the Suez Canal. My data do not throw any light on this suggestion insofar as I find no differences between specimens of *brevipinna* from the Red Sea and others from the eastern North Atlantic, which latter might equally well have been the source of the Mediterranean stock.

Material examined.—SU 52761, female embryo, 408 mm, Brazil, Espirito Santo, Vitória; IFAN 56-114, female embryo, 475 mm, Senegal, Zol, 23 April 1956, J. Cadenat; IFAN 56-118, male embryo, 485 mm, Senegal, Zol, 24 April 1956, J. Cadenat; IFAN 56-116, female embryo, 490 mm, Senegal, Zol, 24 April 1956, J. Cadenat; IFAN 56-117, female embryo, 490 mm, Senegal, Zol, 24 April 1956, J. Cadenat; IFAN 56-158, female embryo, 515 mm, Senegal, Zol, 11 May 1956, J. Cadenat; ISZZ 14237, male embryo, 515 mm, Togo, Diel; SU 52758, female embryo, 552 mm, Brazil, Rio de Janeiro; RNH 7373, female, 580 mm, Batavia, 1852, P. Bleeker; USNM 127111, male embryo, 598 mm, Louisiana, Grand Isle; USNM 127133, male embryo, 635 mm, Louisiana, Grand Isle, 10 July 1930, I. Ginsburg; IFAN 56-196, female embryo, 640 mm, Senegal, Zol, 12 July 1956, J. Cadenat; USNM 127112, female embryo, 640 mm, Louisiana, Grand Isle, 10 July 1930, I. Ginsburg; USNM 127132, male embryo, 640 mm, Louisiana, Grand Isle, 10 July 1930, I. Ginsburg; IFAN 56-195, male embryo, 645 mm, Senegal, Zol, 12 July 1956, F. Paraiso; NMV 61-394, female, 672 mm, Brazil, Rio de Janeiro, 1874, Steindachner; BMNH 67.11.28.192, male, 695 mm, Bleeker; ANSP 73246, male, 720 mm, South Africa, Durban, 27 May 1931, H. W. B. Marley; AMS IB.1222, teeth and skin sample from female, 727 mm (holotype of *Uranga nasuta*), Australia, Queensland, Hervey Bay, Urangan, 16 March 1943; RNH 7374, male, 735 mm, Bleeker; BMNH 1927.10.28.1-5, five embryos, 4 males, 710-790 mm, and 1 female, 785 mm, Western Australia, 615 mi N of Fremantle, A. Ehrenreich; ORID 686, male embryo, 750 mm, South Africa, Natal, Inyoni Beach, 18 May 1963; SFRH 831, female, 757 mm, Israel, Haifa Bay, 23 September 1958, A. Ben-Tuvia; IRSN 98, female, 760 mm (paratype of *Aprionodon caparti*), Angola, Pointa do Dandé, 8°30'S, 13°16'E, 5-6 February 1949; RNH 2525, mounted skin, ca. 785 mm [holotype of *Carcharias (Aprion) brevipinna*], Java, H. Kuhl and J. C. van Hasselt; QMB I.6714, male, 785 mm, Australia, Queensland, Cape Cleveland; MRAC 80255, female, 785 mm (paratype of *Aprionodon caparti*), Angola, Pointa do Dandé, 8°30'S, 13°16'E, 5-6 February 1949; USNM 197432, female, 794 mm, Indian or Pacific Oceans, 1962, T. Abe; IRSN 97, male, 813 mm (holotype of *Aprionodon caparti*), Angola, Pointa do Dandé, 8°30'S, 13°16'E, 5-6 February 1949; SU 13898, female, 815 mm, Japan, Sagami Sea, 1904, A. Owston; BMNH 1905.10., female, 840 mm, Japan; NMV (uncat.) male, 847 mm, Red Sea, Suez, 1895-96; DIRU (uncat.), female, 852 mm, South Africa, Algoa Bay; USNM 179109, male, 865 mm, Florida, Sarasota, Siesta Key, 31 March 1963, Cape Haze Marine Laboratory; USNM 197428, female, 878 mm, Indian or Pacific Oceans, 1962, T. Abe; NMV (uncat.), male, 915 mm, Red Sea, Suez, 21 September 1905, Schönbrunn; NMV 2901 (old number), male, 1,020 mm, Red Sea, 1896; USNM 179111, female, 1,036 mm, Florida, Sarasota, Midnight Pass, 31 March 1963, Cape Haze Marine Laboratory; BMNH 1922.1.13.1, female, 1,093 mm, South Africa, Natal, Cape St. Francis, Marley; DIRU, skin of female, 1,170 mm (holotype of *Carcharhinus johnsoni*) South Africa; NMV 61-429, male, 1,198 mm, Sumatra, Padang, 1896, Schild; NMV 2492 (old number), female, 1,290 mm, Red Sea, Suez; AMS IB.1619, two teeth and skin sample from specimen ca. 1,650 mm (holotype of *Longmania calamaria*), Western Australia, Busselton, 15 November 1943, Nicholas, Soulos, and Veale; ORID 593, female, 1,858 mm, South Africa, Natal, Umdoni Park, 30 March 1963.

Also jaws as follows: QMB I.8253, Australia, Queensland; USNM 109957, Florida, Englewood; USNM 110306, Florida, Englewood; USNM 112597, Florida, Salerno.

Carcharhinus sealei (Pietschmann, 1913)
 Figures 23, 24, 25

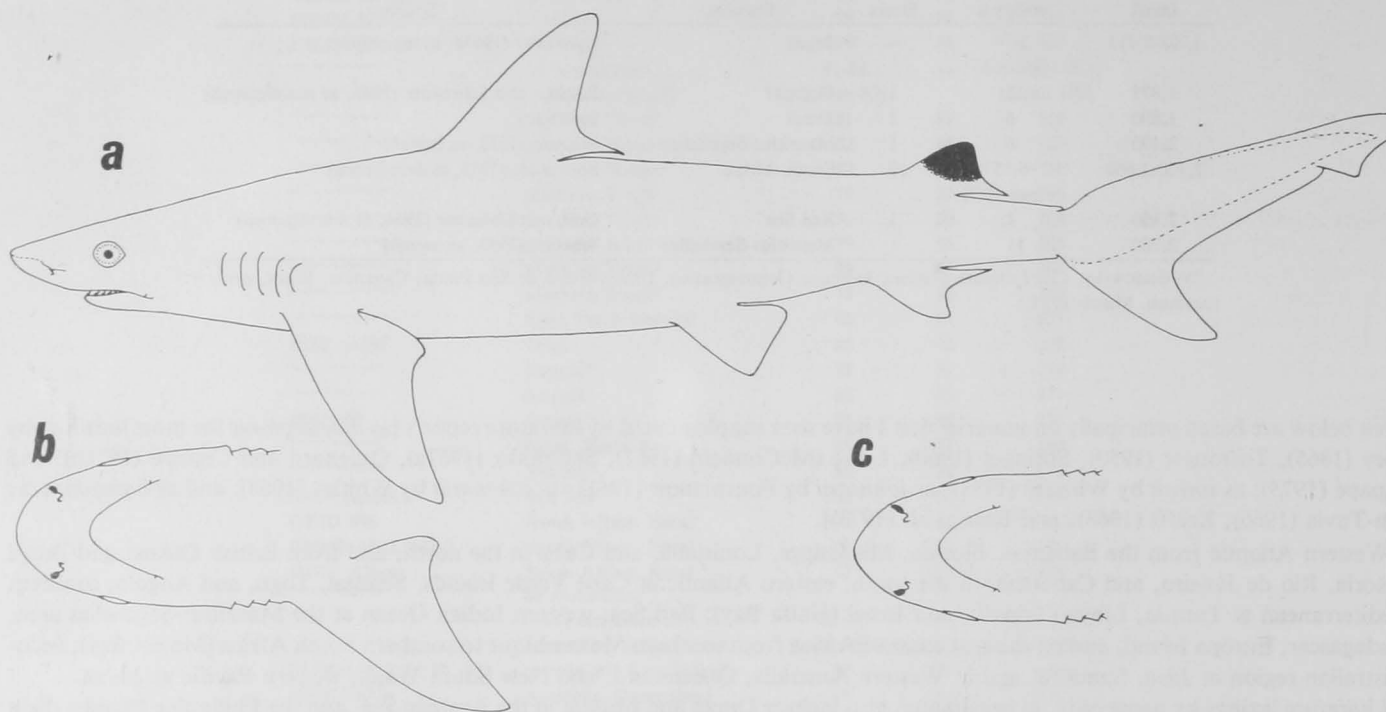


Figure 23.—Western Pacific *Carcharhinus sealei*: a, left side of USNM 151233, 680 mm TL, female from the Philippines (tip of snout and rear tip of second dorsal reconstructed); b, underside of head of same specimen; c, underside of head of SU 13811, 463 mm TL, female from Borneo.

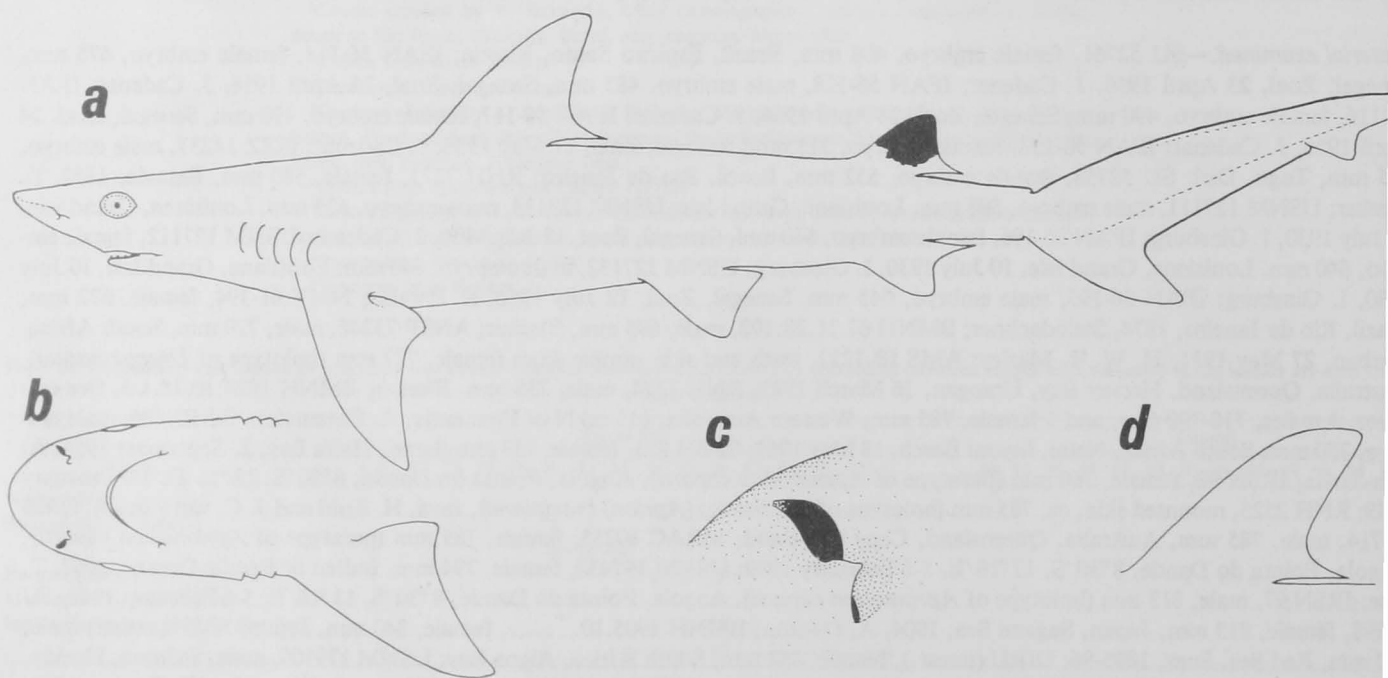


Figure 24.—Western Indian Ocean *Carcharhinus sealei*: a, left side of ANSP 25838, 599 mm TL, female from Natal (rear tip of second dorsal reconstructed); b, underside of head of same specimen; c, enlarged left nostril of same specimen; d, first dorsal fin of ANSP 55298, 368 mm TL, female from Delagoa Bay.

Charcharias borneensis Seale, 1910:263-264, pl. 1, figs. 1-4. Holotype, 372 mm in length to upper caudal origin, Borneo, Sandak
 [Preoccupied by *Carcharias* (*Prionodon*) *borneensis* Bleeker, 1858-59.]

Carcharias sealei Pietschmann, 1913:172, footnote. [Replacement name for *Carcharias borneensis* Seale, 1910.]

Platypodon coatesi Whitley, 1939:234-235, fig. 7. Male, 31 in (787 mm) long, Australia, Queensland.

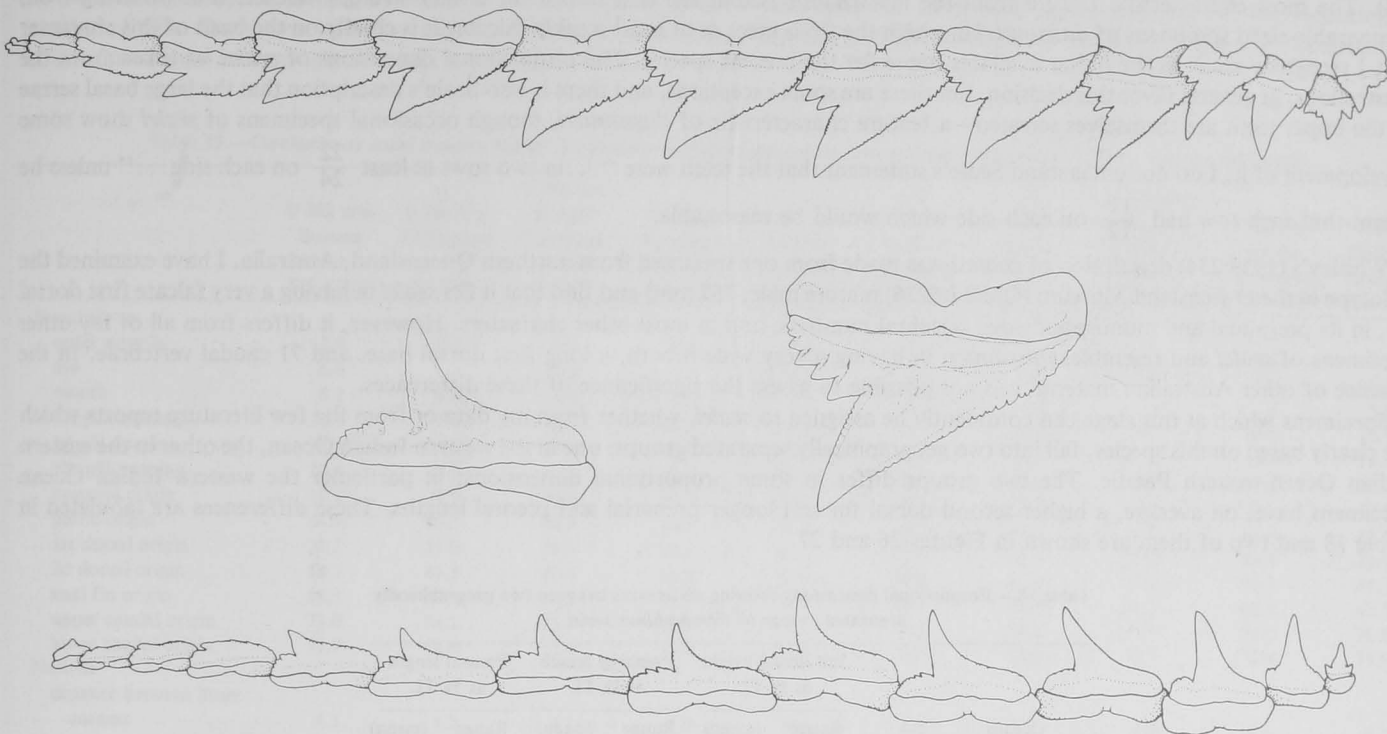


Figure 25.—*Carcharhinus sealei*, USNM 151233, 680 mm TL, female from the Philippines: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

Diagnosis.—Small sharks, up to 0.95 m long, with or without a low interdorsal ridge; second dorsal fin dusky to black but all other fins lacking dark markings and having pale trailing margins; snout short and pointed to rounded; internarial width 1.2-1.6 in preoral length; origin of first dorsal fin about over or slightly behind inner pectoral corner; first dorsal falcate, its apex pointed; origin of second dorsal slightly to noticeably behind anal fin origin; height of second dorsal 2.8-4.3% TL and 0.8-1.3 in length of its rear tip; dental formula usually $\frac{12-2-12}{12-1-12}$ but may be $\frac{12 \text{ or } 13-0 \text{ to } 2-12 \text{ or } 13}{11 \text{ to } 13-0 \text{ to } 2-11 \text{ to } 13}$; upper teeth moderately broad in females and immature males but narrower in

mature males, oblique, deeply notched laterally, medial margins with slightly coarser serrations basally, lateral margins with several very enlarged serrae basally and finer serrations distally; lower teeth oblique, more so in mature males, notched laterally, essentially smooth edged except in adult females where there are fine serrations medially and coarser or enlarged serrae laterally; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 74-85; caudal centra 71-83; total centra 148-167; diplospondyly usually begins above middle third of pelvic base but may be as far back as midway between pelvic rear tip and second dorsal origin; diplospondylous centra either regular in length or with one or more groups of two to five long centra intercalated in the short centra between pelvic base and second dorsal base; penultimate monospondylous centrum 1.1-1.3 times longer than wide.

Carcharhinus sealei is remarkably similar in its color pattern (second dorsal fin obviously dusky to black but all other fins lack dark markings) to the Indo-west Pacific *dussumieri* with which it is sympatric in part of its range, and to a lesser extent it resembles the western Atlantic *acronotus*. Differences between these species are detailed in the account of *dussumieri* (p. 55). Compared with *dussumieri*, *sealei* has a much more falcate first dorsal fin, usually one less tooth on each side of the upper jaw, usually no serrations on the enlarged lateral basal serrae of the upper teeth, a narrower mouth, and a higher pectoral fin length:width ratio. Vertebral numbers provide the surest separation of *sealei* and *dussumieri*.

Nomenclatural discussion.—Problems involved in the separation of *sealei* from *dussumieri* are discussed in the account (p. 57) of the latter species and need not be repeated here except that I would again draw attention to the data tabulated there which emphasize the differences between the species in the numbers of precaudal vertebrae in localities where the two species are sympatric. Additional evidence for separating the species and for the referral of the various nominal species to *sealei* and *dussumieri* is also given in the account of *dussumieri*.

Among the specimens examined in the present study and referred to *sealei* are two of the syntypes of *menisorrah* Valenciennes in Müller and Henle, 1841. These, however, have no effect on the nomenclature of *sealei* because, as I have noted elsewhere in this account (p. 160), the type series of *menisorrah* included two species, and I have selected as lectotype a specimen synonymous with *falciformis*.

The name *sealei* was proposed in a footnote by Pietschmann (1913:172) as a replacement name for *borneensis* Seale, 1910 which Pietschmann correctly noted was preoccupied by *borneensis* Bleeker, 1858-59. Pietschmann made no further comment on *sealei*. Seale's account of his *borneensis* (1910:263) was based on one specimen, apparently female, 372 mm in length to upper caudal origin, taken at Sandakan, Borneo. This specimen was deposited as No. 2720 in the collection of the Bureau of Science, Manila, Philippine Islands, but, as far as I can ascertain, this collection was destroyed by fire during World War II. In consequence the interpretation of *sealei* can be made only from Seale's account. Seale's description is good and is accompanied by excellent illustrations (his pl. 1, figs.

1-4). The most characteristic feature from the illustrations is that the first dorsal fin is very strongly falcate, thus differing from comparable-sized specimens of *dussumieri* in which the fin is erect or at most weakly falcate. It is chiefly on the basis of this character that I recognize *sealei* as the oldest available name for the present species. The proportional dimensions of *sealei*, as taken from the illustrations, in general favor this decision, but there are some exceptions, and there is also Seale's description that the large basal serrae of the upper teeth are themselves serrated—a feature characteristic of *dussumieri*, though occasional specimens of *sealei* show some development of it. I do not understand Seale's statement that the teeth were "...in two rows at least $\frac{22}{24}$ on each side..." unless he meant that each row had $\frac{11}{12}$ on each side which would be reasonable.

Whitley's (1939:234) description of *coatesi* was made from one specimen from northern Queensland, Australia. I have examined the holotype in the Queensland Museum (QMB I.6226, mature male, 782 mm) and find that it fits *sealei* in having a very falcate first dorsal fin, in its precaudal and monospondylous vertebral numbers, and in most other characters. However, it differs from all of my other specimens of *sealei* and resembles *dussumieri* in having a very wide mouth, a long first dorsal base, and 71 caudal vertebrae. In the absence of other Australian material it is not possible to assess the significance of these differences.

Specimens which at this stage can confidently be assigned to *sealei*, whether from my data or from the few literature reports which are clearly based on this species, fall into two geographically separated groups: one in the western Indian Ocean, the other in the eastern Indian Ocean-western Pacific. The two groups differ in some proportional dimensions; in particular the western Indian Ocean specimens have, on average, a higher second dorsal fin and longer preanal and preoral lengths. These differences are tabulated in Table 18 and two of them are shown in Figures 26 and 27.

Table 18.—Proportional dimensions showing differences between two geographically separated groups of *Carcharhinus sealei*.

Oceans		2nd dorsal height as % TL		Prenarial length as % TL		Preoral length as % TL	
		Range	(mean)	Range	(mean)	Range	(mean)
Western Indian	(n = 15) ¹	3.1-4.2	(3.8)	2.6-3.7	(3.2)	6.1-7.3	(6.8)
Eastern Indian- western Pacific	(n = 11)	2.8-3.6	(3.2)	2.2-3.0	(2.7)	5.3-6.7	(5.9)

¹Including 12 specimens from Zanzibar, reported on by Wheeler (1960) as *menisorrah*.

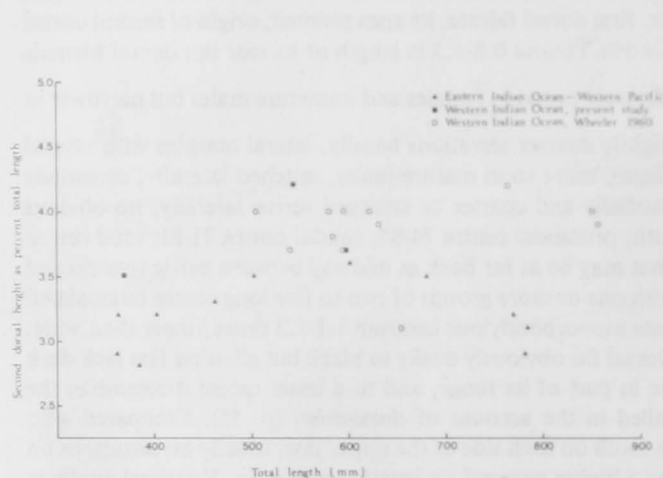


Figure 26.—Second dorsal height as percent of total length versus total length in *Carcharhinus sealei* from the two sides of the Indian Ocean.

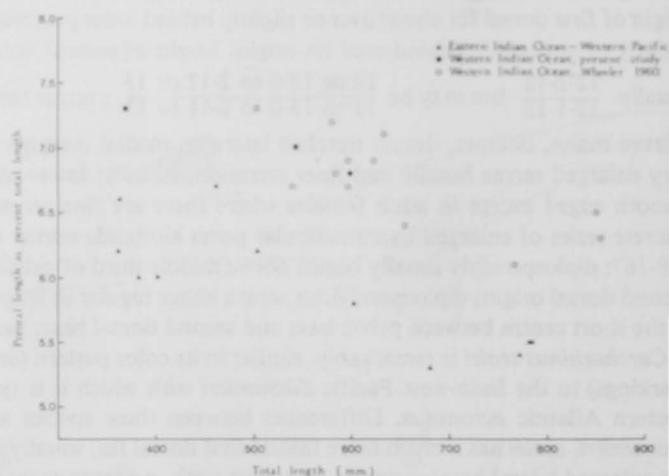


Figure 27.—Preoral length as percent of total length versus total length in *Carcharhinus sealei* from the two sides of the Indian Ocean.

I find no other differences between the groups either in vertebral numbers or in morphology, except that firstly, the western Indian Ocean specimens are, in general, smooth backed whereas eastern Indian Ocean-western Pacific specimens usually have a low, inconspicuous dermal ridge between the two dorsal fins, and secondly, the western Indian Ocean specimens usually have the anterior margin of the eye slightly forward of the front of the mouth rather than behind it as in the eastern Indian Ocean-western Pacific specimens.

The above differences between the groups, although slight, could justifiably be regarded as meriting formal nomenclatural recognition at the subspecific level. However, I favor recognizing them only informally at this stage (thus avoiding the possibility of burdening the literature with names that may prove to be unnecessary) because it seems likely that the two groups could represent merely the end segments of a continuously distributed Indo-west Pacific species. Their apparent discontinuity, and differences, may well be bridged by specimens from the northern borders of the Indian Ocean. The related *dussumieri* is present in at least part of this region—the Persian Gulf and eastwards to India—and it is conceivable that some of the records attributed to that species could have been based on *sealei*. One such example is from Day (1878, pl. 187, fig. 2), who illustrated, as *dussumieri*, a specimen from Malabar, India, which appears to be *sealei*. However, some aspects of the illustration do not engender confidence in the details or the proportions, and I hesitate to identify it with certainty.

Description (see also Tables 19, 20).—Small sharks, apparently not exceeding 1 m TL. Midline of back between dorsal fins smooth (most western Indian Ocean specimens) or with a low, inconspicuous dermal ridge perhaps accentuated by preservation in some specimens. Upper precaudal pit strongly developed, lower pit weak.

Table 19.—*Carcharhinus sealei* (eastern Indian Ocean-western Pacific specimens), proportional dimensions in percentage of total length.

	♀ 362 mm Borneo Sandakan SU 27726	♀ 364 mm Philippines Cebu SU 27561	♀ 386 mm Borneo Sandakan CNHM 21879	♂ 402 mm Singapore UZMK PO 677	♀ 463 mm Borneo Sandakan SU 13811	♂ 503 mm Gulf of Thailand GVF 2467	♀ 602 mm Cochin China MNHN 7803	♀ 680 mm Philippines Cebu USNM 151233	♂ 782 mm Australia Queensland QMB 1.6226	♂ 785 mm Gulf of Thailand GVF 2563
Snout tip to										
outer nostrils	2.8	3.0	2.9	3.0	3.0	2.7	2.5	2.2	2.4	2.7
eye	6.6	6.9	6.9	6.2	6.9	6.4	6.3	5.9	5.9	6.3
mouth	6.2	6.6	6.0	6.0	6.7	6.2	5.8	5.3	5.5	5.5
1st gill opening	16.3	17.3	15.0	16.2	16.4	16.6	16.1	15.1	16.8	16.3
3d gill opening	17.9	19.6	17.6	18.7	19.2	19.1	18.4	17.7	—	18.8
5th gill opening	20.4	21.8	19.8	20.4	20.9	21.2	20.5	19.7	21.1	20.7
pectoral origin	19.6	20.9	19.0	20.0	20.3	20.3	20.2	19.0	20.1	19.9
pelvic origin	44.8	45.3	44.6	44.6	46.6	44.7	45.6	47.2	45.8	46.5
1st dorsal origin	29.5	31.0	29.5	29.2	31.3	29.2	29.2	30.0	29.3	29.9
2d dorsal origin	59.7	61.5	60.7	60.0	61.6	60.8	61.2	63.0	62.3	64.2
anal fin origin	58.3	59.9	57.3	58.4	60.5	59.2	59.6	60.9	60.5	62.3
upper caudal origin	73.0	74.2	73.1	72.3	74.5	73.5	74.0	75.8	75.0	76.8
lower caudal origin	71.9	72.6	71.4	72.0	73.7	72.6	72.9	74.7	74.0	75.9
Nostrils										
distance between inner corners	4.1	4.2	4.1	4.0	4.4	4.2	3.8	4.3	4.6	4.1
Mouth										
width	6.1	6.3	6.2	6.0	6.0	6.5	6.1	6.5	7.9	6.2
length	4.4	4.4	4.3	4.2	4.2	4.4	4.2	4.3	4.3	4.8
Labial furrow lengths										
upper	—	—	0.5	0.4	0.4	0.2	0.4	0.4	0.3	0.4
lower	—	—	0.4	0.5	0.3	0.4	0.4	0.3	0.2	0.3
Gill opening lengths										
1st	1.9	2.1	2.6	2.1	2.6	2.2	2.2	2.4	2.6	2.4
3d	2.3	2.5	3.1	2.5	3.2	2.6	2.4	3.1	2.9	2.9
5th	1.9	1.9	2.1	2.0	2.3	2.1	2.1	2.1	2.2	2.4
Eye										
horizontal diameter	2.8	2.9	2.7	2.9	2.7	2.4	2.2	2.3	2.3	2.2
1st dorsal fin										
length of base	9.1	8.8	8.8	8.8	9.0	9.4	8.6	9.0	9.7	9.0
length posterior margin	4.2	4.1	4.2	4.1	4.6	—	4.5	4.9	4.5	3.9
height	8.8	9.1	9.1	9.7	10.1	10.1	11.0	10.1	9.8	9.5
2d dorsal fin										
length of base	4.8	4.7	4.2	4.4	4.8	5.0	4.2	4.6	4.3	4.5
length posterior margin	3.7	3.8	3.6	3.2	3.7	—	3.5	—	3.3	3.2
height	2.9	3.2	2.8	3.2	3.3	3.5	3.6	3.5	2.9	3.1
Anal fin										
length of base	5.5	4.8	5.6	5.3	5.5	6.2	5.4	5.9	5.1	5.4
length posterior margin	3.6	3.6	3.5	3.1	3.4	2.6	3.3	3.8	3.3	3.2
height	3.6	3.6	3.0	3.5	4.1	3.7	3.2	3.5	3.4	3.3
Pectoral fin										
length of base	5.8	5.5	5.4	5.3	5.8	5.8	5.1	5.7	6.0	5.9
length anterior margin	16.0	15.1	16.0	15.4	17.1	16.2	15.9	17.9	15.8	15.2
length distal margin	9.9	10.4	10.6	9.9	12.7	11.3	12.2	11.6	11.1	11.8
greatest width	8.3	—	8.2	8.0	9.3	9.2	8.8	9.1	—	9.0
Pelvic fin										
length of base	5.4	4.9	4.7	4.6	5.2	5.4	5.1	5.0	5.7	5.5
length anterior margin	6.6	6.3	5.7	6.0	6.7	6.7	6.0	7.0	6.5	5.9
length distal margin	4.7	4.7	4.7	4.7	5.4	5.3	5.0	5.1	5.4	5.2
length of claspers	—	—	—	2.0	—	2.6	—	—	8.7	8.8
Caudal										
length of upper lobe	27.1	26.4	27.0	27.3	26.4	27.0	26.4	24.8	25.0	23.9
length of lower lobe	12.0	11.5	11.1	12.2	12.1	12.5	11.8	12.5	11.1	11.3
Trunk at pectoral origin										
width	10.4	10.4	10.4	9.7	10.8	10.7	10.1	10.3	11.0	10.2
height	9.8	10.2	10.1	9.2	10.1	10.5	9.4	10.3	10.3	10.7
Dental formula	13-12 12-1-12	12-1-12 12-1-12	12-2-12 12-1-12	13-1-13 12-1-12	12-2-12 12-1-12	—	13-1-12 12-1-12	13-2-13 13-1-13	12-2-12 12-1-12	13-2-13 12-2-12
Vertebrae										
precaudal	81	84	75	77	77	77	—	81	77	79
caudal	80	82	80	74	78	77	—	80	71	73
total	161	166	155	151	155	154	—	161	148	152

¹Holotype of *Platypodon coatesi*.

Table 20.—*Carcharhinus sealei*, (western Indian Ocean specimens), proportional dimensions in percentage of total length.

	♀ 368 mm	♂ 506 mm	♂ 540 mm	♀ 545 mm	♂ 580 mm	♂ 595 mm	♀ 599 mm	♂ 635 mm	♂ 767 mm	♂ 855 mm
	East Africa	East Africa	East Africa	South Africa	East Africa	East Africa	South Africa	East Africa	East Africa	East Africa
	Delagoa Bay	East Africa	East Africa	Durban	East Africa	East Africa	Natal	East Africa	East Africa	East Africa
	ANSP 55298	Zanzibar	Zanzibar	DIRU	Zanzibar	Zanzibar	ANSP 25838	Zanzibar	Zanzibar	Zanzibar
Snout tip to										
outer nostrils	3.3	3.4	3.7	3.5	3.4	3.0	3.0	3.5	2.9	3.0
eye	7.6	—	—	6.8	—	—	6.4	—	—	—
mouth	7.3	7.3	6.7	7.0	7.2	6.7	6.8	7.1	6.1	6.3
1st gill opening	16.9	15.4	14.4	16.2	15.8	15.1	16.3	16.2	15.4	15.8
3d gill opening	19.0	—	—	18.2	—	—	18.7	—	—	—
5th gill opening	21.0	20.2	20.0	20.2	21.4	19.5	21.0	19.8	19.8	19.9
pectoral origin	20.1	19.4	—	19.8	—	—	19.9	—	—	—
pelvic origin	46.8	44.5	44.5	45.6	44.8	43.7	44.9	43.0	43.5	46.8
1st dorsal origin	30.5	28.9	26.3	28.8	29.3	28.6	29.4	28.3	27.4	28.7
2d dorsal origin	59.6	58.9	59.6	60.4	60.3	59.2	59.6	59.8	60.4	62.0
anal fin origin	59.3	58.3	58.3	59.7	60.9	57.6	59.8	58.3	60.0	63.2
upper caudal origin	73.1	73.5	73.5	73.7	74.4	73.5	73.8	74.0	75.5	75.6
lower caudal origin	72.3	71.9	73.5	73.0	74.7	71.9	73.0	71.7	73.7	76.1
Nostrils										
distance between inner										
corners	4.9	4.7	4.4	4.6	5.2	4.5	4.7	4.9	4.2	4.2
Mouth										
width	6.4	6.3	5.6	6.6	6.0	6.1	6.4	6.3	6.1	6.2
length	4.5	—	3.7	3.9	3.5	3.4	3.8	3.1	3.5	4.0
Labial furrow lengths										
upper	—	—	—	—	—	—	0.5	—	—	—
lower	—	—	—	—	—	—	0.4	—	—	—
Gill opening lengths										
1st	2.2	—	—	2.4	—	—	2.3	—	—	—
3d	2.7	3.0	2.4	2.7	3.1	2.7	2.7	2.8	2.6	2.9
5th	2.2	—	—	2.1	—	—	2.2	—	—	—
Eye										
horizontal diameter	—	2.4	2.2	2.3	2.2	2.4	2.6	2.2	—	—
1st dorsal fin										
length of base	8.7	8.3	9.3	9.2	9.0	9.4	8.8	8.8	9.1	9.0
length posterior margin	4.6	4.3	4.1	4.2	4.5	4.0	4.7	4.4	4.3	4.2
height	8.2	10.7	9.3	9.7	10.7	9.4	9.7	10.2	9.1	9.4
2d dorsal fin										
length of base	6.1	5.1	4.6	4.8	5.2	5.0	5.0	5.5	5.2	4.8
length posterior margin	3.8	3.8	3.7	3.6	3.4	3.5	3.5	3.1	4.0	4.7
height	3.5	4.0	3.7	4.2	4.0	3.7	4.3	3.9	4.2	3.9
Anal fin										
length of base	6.0	5.3	5.6	5.9	5.2	5.0	5.7	4.7	4.8	4.3
length posterior margin	3.8	3.6	3.3	3.5	4.0	3.4	3.7	3.9	3.9	4.0
height	3.8	3.6	3.7	3.7	3.4	3.2	3.7	3.3	3.7	3.5
Pectoral fin										
length of base	5.4	5.3	—	5.7	—	—	5.8	—	—	—
length anterior margin	16.7	14.8	14.4	16.0	15.5	13.9	16.3	14.7	13.3	13.5
length distal margin	10.6	—	—	12.7	—	—	11.3	—	—	—
greatest width	8.7	—	—	—	—	—	8.9	—	—	—
Pelvic fin										
length of base	5.0	—	—	4.9	—	—	6.0	—	—	—
length anterior margin	7.1	6.3	6.5	7.0	6.7	6.7	7.3	6.3	6.1	6.7
length distal margin	4.5	4.5	4.4	5.1	4.5	4.6	5.2	5.5	5.5	5.3
length of claspers	—	—	2.8	—	—	3.4	—	3.5	3.9	11.5
Caudal										
length of upper lobe	26.9	27.1	25.9	26.3	27.6	27.7	26.6	27.4	26.1	23.6
length of lower lobe	11.8	12.1	11.5	11.4	12.1	11.3	11.8	12.0	9.4	11.1
Trunk at pectoral origin										
width	10.3	—	—	11.6	—	—	10.8	—	—	—
height	10.0	—	—	10.5	—	—	9.4	—	—	—
Dental formula	12-1-12	—	—	12-2-12	—	—	12-2-12	—	—	—
	12-1-12			12-1-12			11-1-11			
Vertebrae										
precaudal	78	—	—	—	—	—	75	—	—	—
caudal	83	—	—	—	—	—	80	—	—	—
total	161	—	—	—	—	—	155	—	—	—

¹Measurements from Wheeler (1960:273).

Dermal denticles close-packed, slightly overlapping (more so in large than in small specimens), subcircular in outline in small specimens but more ovoid to rhomboid in large specimens, each with three longitudinal ridges and three or five rather strong posterior marginal teeth in small specimens but with five ridges and teeth in large specimens.

Snout rather short, varying from bluntly pointed to rounded in contour. Anterior margin of eye is slightly behind front of mouth in eastern Indian Ocean-western Pacific specimens but usually slightly forward of mouth in western Indian Ocean specimens. Nostrils oblique, with broadly ovate apertures, the anterior margin of each with a well-developed, sharply pointed lobe.

Dental formula $\frac{12-1 \text{ or } 2-12}{12-1-12}$ in 6 of 13 specimens counted; $\frac{13-1 \text{ or } 2-13}{12-0 \text{ to } 2-12}$ in 3; $\frac{12-2-12}{11-1-11}$ in 1; and within the range $\frac{12 \text{ or } 13-0 \text{ or } 1-12 \text{ or } 13}{12 \text{ or } 13-1-12 \text{ or } 13}$ in the remaining 3. Teeth sexually dimorphic in adult specimens. Upper teeth moderately broad, oblique, their lateral margins deeply notched, their medial margins convex basally but straight to concave distally; two to five large serrae basally on the lateral margin of each tooth; medial margins of teeth serrated, the serrations rather coarse and irregular, lateral margins smooth in small specimens but serrated in larger, the serrations usually not extending onto the large basal serrae; one or two (occasionally none) smaller symphysial teeth. Lower teeth narrow, oblique except perhaps for the first series on each side of center of mouth, their lateral margins deeply notched, their medial margins concave; in adult males the first four or five lower teeth on each side of the symphysis are more slender, oblique, and flexuous than those of adult females (this occurs to a less marked degree in the upper teeth also); medial and lateral margins smooth, or nearly so, in small specimens and in adult males, but in adult females the medial margins are to some extent finely and sparsely serrated; some of the more lateral lower teeth in adult females also have large and irregular serrae basally on their lateral margins, and these are foreshadowed in some of the smaller specimens; one, two, or no small symphysial teeth.

First dorsal fin moderately high, greatly narrowed in lateral view towards the apex, strongly falcate, a vertical from its apex falling at least two-thirds along the rear tip of the first dorsal; origin of first dorsal usually above or slightly behind the inner (posterior) corner of pectoral fin, but occasionally slightly anterior to it. Second dorsal fin moderately high but relatively short, about equal to or larger than the anal fin; length of second dorsal rear tip 0.96-1.31 (mean 1.15) times second dorsal height in 9 eastern Indian Ocean-western Pacific specimens, 0.80-1.22 (mean 0.97) in 15 western Indian Ocean specimens; origin of second dorsal virtually above or slightly behind anal fin origin to as far back as anterior one-third of anal base. Pectoral fins moderately short, falcate, with pointed tips; origin of pectorals below the fourth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches from three-fourths along first dorsal base to almost to first dorsal axil.

Color after preservation in alcohol is gray or brownish gray above, paler below; all fins except the second dorsal are at most only slightly darker than the upper trunk color, though their trailing edges are pale; most of second dorsal fin is dusky to black except for the rear tip which behind the axil is white.

Vertebral counts of 11 specimens are given in Tables 19 and 20 and of another 25 specimens in Table 21.

Table 21.—Vertebral numbers in 25 specimens of *Carcharhinus sealei*.

Specimens		Precaudal	Caudal	Total
GVF 2132	Gulf of Thailand	79	77	156
BMNH (Uncat.)	Malaya, Selangor	78	75	153
SU 8027	Sumatra	79	77	156
	22 specimens,	74-85	—	152-167
	South Africa, Natal ¹	(mean 79.4)		(mean 161.0)
Range (including counts from Tables 19 and 20)		74-85	71-83	148-167

¹Counts from Bass et al. (1973)

Centrum diameter greater than centrum length except for last few monospondylous centra at posterior of abdomen. Diplospondyly begins variously above anterior third of pelvic base or posteriorly to as far back as about midway between pelvic and second dorsal fins. Diplospondylous centra regular in length in 6 of 14 specimens radiographed, but in the other 8 there are one or more groups of two to five slightly to considerably elongated centra interposed between the "normal" shorter centra. These interposed groups of centra occur in the region between the pelvic and second dorsal fins or even slightly behind the second dorsal fin. Posteriorly to them, along the caudal peduncle and on the caudal axis, the centra are regular in length. Specimens with regular diplospondylous precaudal centra have been examined from the Gulf of Thailand, Borneo, Sumatra, and South Africa. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 1.07-1.29 (mean 1.17) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.11-2.14 (mean 1.44) in 14 specimens.

The smallest, apparently free-living specimen that I have seen was 330 mm TL (from Java) and the largest embryo was 364 mm (from the Philippines). Bass et al. (1973) reported a free-living specimen of 350 mm from Mozambique (Beira) but noted that size at birth can be up to 450 mm judging by a verbal record⁶ of two embryos of 440 and 450 mm from Delagoa Bay. Of the few males examined in the present study, two up to 503 mm long were immature with clasper lengths of 2.0-2.6% TL, while four others of 765-785 mm, from such widely spaced localities as the Gulf of Thailand, Sumatra, and Queensland, Australia, were mature with clasper lengths of 8.7-8.9%. Wheeler (1960), who gave data on eight males and four females, as *menisorrah*, from Zanzibar stated that males mature at about 850 mm. His data show that six males of 540-767 mm had clasper lengths of 2.8-3.9% TL, and hence would be immature, while two others of 850 and 855 mm had clasper lengths of 10.6 and 11.5% and were mature. (These clasper length percentages are higher than any of mine, suggesting that Wheeler's method of measuring claspers differed from mine.) Bass et al. (1973) noted that their largest immature male from the east coast of southern Africa was 690 mm, and that eight mature males were 750 mm or longer. Information is scant on size at maturity and reproduction in the female. Of specimens seen by me, one female of 680 mm from the Philippines was near maturity judging by the degree of development of the oviducts. The smallest of 10 mature females examined by Bass et al. (1973) was 750 mm

⁶Bass et al. (1973:71) report a personal communication to them from Caixeiro.

long. The same authors noted that "The number of embryos varies between one and two. Records in the present study include one female with a single embryo and five with two embryos each. . . . Mating . . . appears to take place in summer with birth possibly about nine months later." Wheeler (1960) recorded an embryo of 240 mm from Lamu, north of Zanzibar, but did not state if it was the only one in the litter.

The largest specimens examined by me were a female of 680 mm and a male of 785 mm. Maximum sizes reported in the literature are considerably greater than these. Wheeler (1960) recorded a male of 855 mm, Bass et al. (1973) a male of 900 mm and a female of 920 mm (but the latter given as 940 mm in their list of material), and Marshall (1964, as *coatesi*) illustrated a Queensland male of 37½ in (953 mm).

Distribution (see also Material examined).—Present records give *sealei* a disjunct distribution involving the western Indian Ocean on the one hand and the eastern Indian Ocean-western Pacific on the other. The distribution is principally tropical but extends to about lat. 30°S (Durban) in the western Indian Ocean. Localities given below are based on specimens that I have seen supplemented by others reported in Wheeler (1960) and Bass et al. (1973).

Eastern Indian Ocean-western Pacific at the Philippine Islands, Vietnam, and Gulf of Thailand in the north and southwards in the Malayan region (Malacca, Selangor), Singapore, Borneo, Sumatra, Celebes, Java, New Guinea (Yapen Island), and eastern Australia at northern Queensland.

Western Indian Ocean from the African coast at about lat. 2°30'S (Lamu) and southwards at Zanzibar, the west coast of Madagascar (single specimen taken at surface over 1,260 m but not far from shallower depths, reported in Bass et al. 1973), Mozambique (Beira, Bazaruto Island, Delagoa Bay), and South Africa (Natal to at least as far south as Durban). Offshore it is present, but rare, at the Seychelles according to Smith and Smith (1963). I am unable to verify Garman's (1913) listing of it from Mauritius.

Material examined.—RNH 2523, mounted skin of male, 330 mm [syntype of *Carcharias (Prionodon) menisorrah*], Java, Kuhl and van Hasselt; RNH 7376, male, 343 mm, and female, 515 mm, Indian Archipelago, Bleeker; RNH 4229, female, 355 mm, and male, 360 mm, Macassar, 1849, D. M. Piller; SU 27726, female embryo, 362 mm, Borneo, Sandakan, A. W. Herre; SU 27561, female embryo, 364 mm, Philippine Islands, Cebu, 26 August 1931, A. W. Herre; UZMK PO 691, female, 365 mm, Malacca, 25 November 1919, M. Jensen; ANSP 55298, female, 368 mm, Portuguese East Africa, Delagoa Bay, 1922, H. W. B. Marley; UZMK PO 696, male, 375 mm, Gulf of Thailand, Koh Chang, 19 January 1900, T. H. Mortensen; CNHM 21879, female, 386 mm, Borneo, 2 July 1929, Crane Pacific Expedition; SMNS 817, male, 394 mm, Indian Archipelago, Bleeker; MSNG C. E. 23319, male, 395 mm, Borneo, 1886; BMNH (uncat.), male, 395 mm, Selangor; UZMK PO 677, male, 402 mm, Singapore, Andréa; RNH 4230, male, 450 mm, Macassar, 1849, D. M. Piller; SU 13811, female, 463 mm, Borneo, Sandakan, 1 July 1929, A. W. Herre; AMS B 5052, male, 478 mm, Selangor; SU 8027, male, 491 mm, Sumatra, Padang, H. W. Fowler; GVF 2467, male, 503 mm, Gulf of Thailand, Trat Province, about 2-3 mi offshore V and WSW of Goh Chang, 12 January 1961; NMV (—), male, 525 mm, Batavia, 1855; IRSN 2545, female, 533 mm, Java, Samarang, January 1929, Prince Leopold; RNH 2521, mounted skin of male, 535 mm [syntype of *Carcharias (Prionodon) menisorrah*], Java, Kuhl and van Hasselt; DIRU (uncat.), female, 545 mm, South Africa, Durban, 14 February 1961, A. R. Thorpe; RNH (uncat.), female, 555 mm, New Guinea, Yapen Island, Cape Rainbauri, 1954-55, L. D. Brongersma; BMNH 67.11.28.206, male, 565 mm, Bleeker; NMV (—), female, 595 mm, Java, *Novara*; ANSP 25838, female, 599 mm, South Africa, Natal, 1935, H. W. B. Marley; MNHN 7803, female, 602 mm, Cochin China, Harmand; RNH 7384, female, 612 mm, Bleeker; USNM 151233, female, 680 mm, Philippine Islands, Cebu market, 16 August 1909, *Albatross*; NMV 61-360, mature male, 765 mm, Sumatra, Padang, Schild; GVF 2132, mature male, 772 mm, Gulf of Thailand, Prachuap Khiri Khan Province, 5 April 1960; QMB I.6226, mature male, 782 mm (holotype of *Platypodon coatesi*), Australia, Queensland, Hinchinbrook Passage, April 1938, G. Coates; GVF 2563, mature male, 780 mm, Gulf of Thailand, Surat Thani Province, ca. 9°32'15"N, 100°09'45"E, 6-8 May 1961.

Carcharhinus dussumieri (Valenciennes in Müller and Henle, 1841)

Figures 28, 29, 30, 31, 32

Carcharias (Prionodon) dussumieri Valenciennes in Müller and Henle, 1841:47-48, pl. 19. One specimen from China in the Berlin Museum; two specimens from Bombay, India; and one from Pondicherry, India, in the Paris Museum.

Carcharias (Prionodon) tjutjot Bleeker, 1852:36-37, pl. 1, fig. 4. Two males, 590 and 615 mm, Java, in sea at Batavia.

Carcharias (Prionodon) javanicus Bleeker, 1852:38-39, pl. 2, fig. 5. Female, 470 mm, Java, in sea at Batavia.

Carcharias malabaricus Day, 1873:529-530. One specimen, 15 in (381 mm) long, from Cochin, India, and two specimens, 16 in (406 mm) long, from Calicut (= Kozhikode), India.

Diagnosis.—Small sharks, up to about 1 m long, with a low interdorsal ridge; second dorsal fin dusky to black but all other fins lack iridescent dark markings and having pale trailing margins; snout of moderate length and pointed to sharply rounded; internarial width 1.1-1.6 preoral length; origin of first dorsal fin over posterior half of inner pectoral margin; first dorsal erect, its apex sharply rounded and pointed; origin of second dorsal over or slightly behind anal fin origin; height of second dorsal 2.6-4.0% TL and 1.0-1.5 in length of first rear tip; dental formula usually $\frac{13-2-13}{13 \text{ or } 14-1-13 \text{ or } 14}$ but may be $\frac{12 \text{ to } 14-0 \text{ to } 3-12 \text{ to } 14}{11 \text{ to } 15-0 \text{ to } 2-11 \text{ to } 15}$ upper teeth moderately broad in females as in immature males but narrower in mature males, oblique, deeply notched laterally, uniformly serrated except for bases of lateral margins which carry several very enlarged serrae that are themselves serrated; lower teeth oblique, more so in mature males, notched laterally and serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 54-74; caudal centra 53-79; total centra 109-150; diplospondyly usually begins from above pelvic axil to about midway between pelvic rear tip and second dorsal origin but may be as far forward as anterior third of pelvic base or as far back as midway along second dorsal base; diplospon-

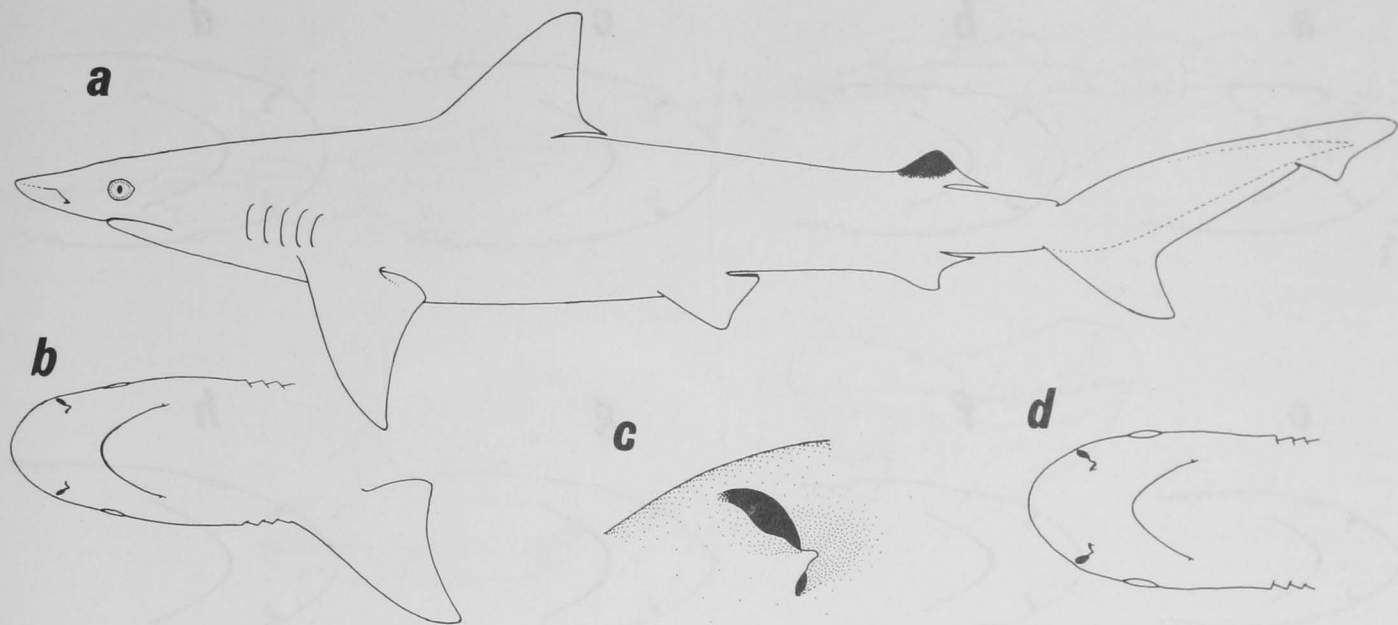


Figure 28.—*Carcharhinus dussumieri*, UMMZ 177112, 660 mm TL, male from Java: *a*, left side (apex of anal fin and tip of lower caudal lobe reconstructed); *b*, underside of head; *c*, enlarged left nostril; *d*, underside of head of MCZ 1386, 310 mm TL, female from Java.

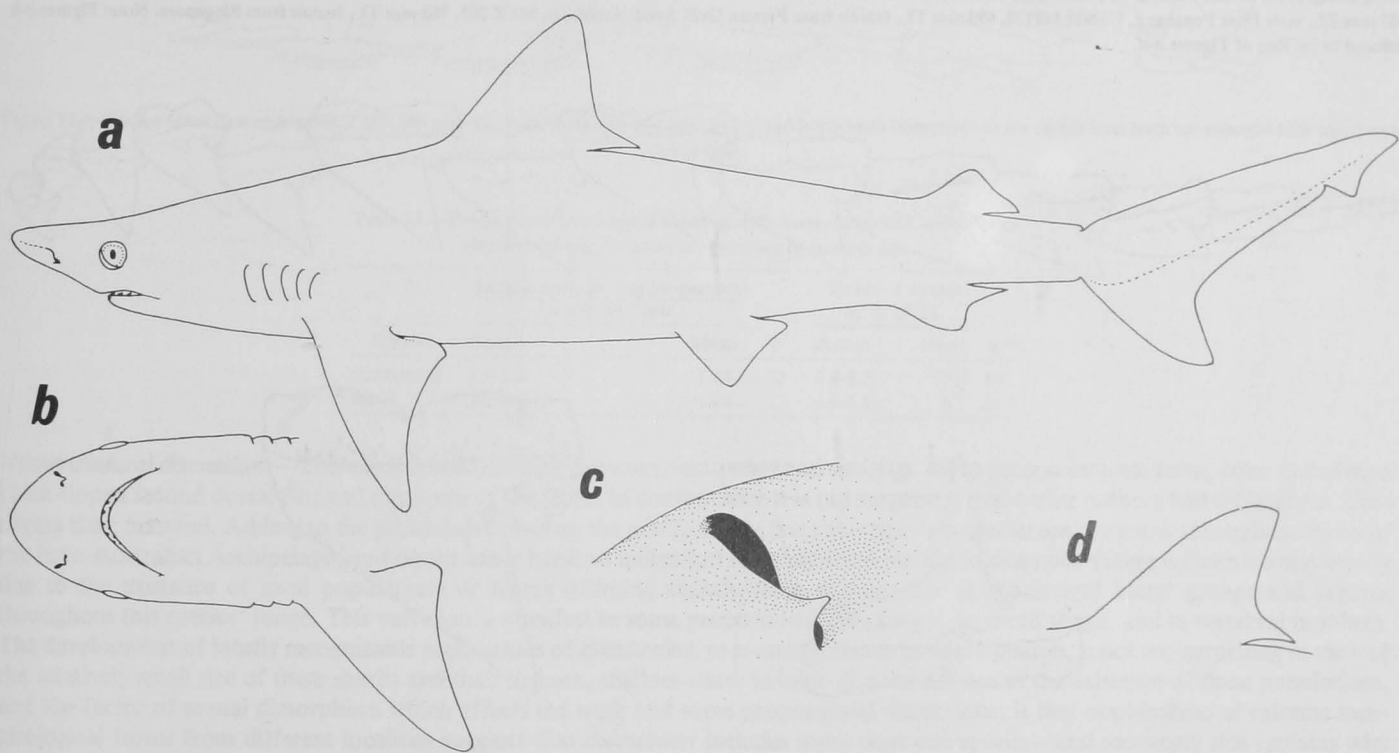


Figure 29.—*Carcharhinus dussumieri*, GVF 2706, 785 mm TL, female from Gulf of Thailand: *a*, left side (black mark on second dorsal fin not shown in figure); *b*, underside of head; *c*, enlarged left nostril; *d*, first dorsal fin of CNHM 21878, 353 mm TL, male from Borneo.

dylous centra usually not regular in length between pelvic base and second dorsal base, where there may be from one to six alternating pairs of short and long centra; likewise on caudal axis the centra are usually irregular with one to four long centra intercalated between short centra; penultimate monospondylous centrum 1.1-1.7 times longer than wide.

The prominently black-tipped second dorsal fin of *dussumieri*, coupled with the absence of dark markings on any other fins, are highly distinctive features matched only in the Indo-Pacific *sealei*. The western Atlantic *acronotus* approaches both these species in many respects, including having a dusky to blackish second dorsal, but its marking is less obvious and there are also dusky margins on the caudal fin and a dusky to black blotch on the snout tip. Vertebral numbers (see under Nomenclatural discussion) provide the surest means of separating *dussumieri* and *sealei*. Other differences of more general application are the shape of the first dorsal fin (erect in *dussumieri*, falcate in *sealei*), the number of teeth (usually one more tooth on each side of the upper and lower jaws in *dussumieri* than

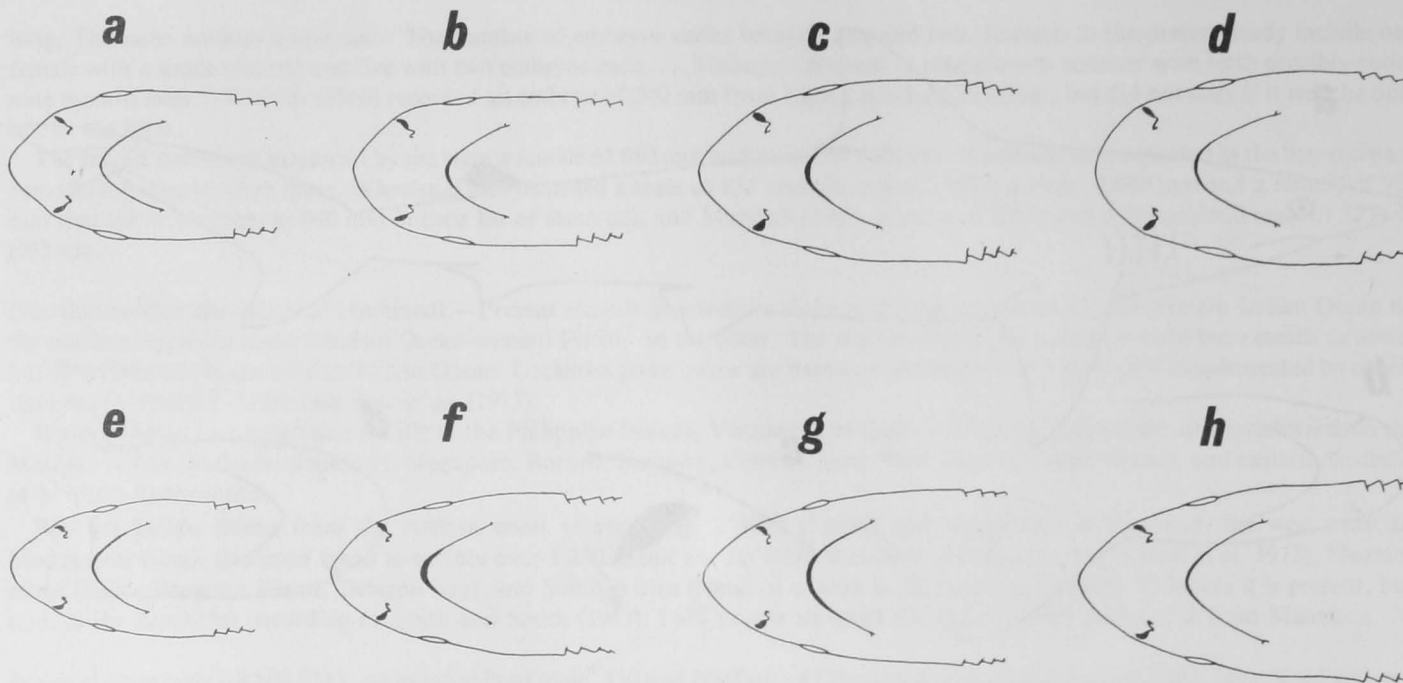


Figure 30.—Variation in snout shape and proportions in *Carcharhinus dussumieri*: a, SU 31254, 300 mm TL, female from Hong Kong; b, SU 31254, 304 mm TL, male from Hong Kong; c, SU 27726, 348 mm TL, male from Borneo; d, CNHM 21878, 353 mm TL, male from Borneo; e, UMMZ 177114, 580 mm TL, female from Japan; f, MCZ 109687 mm TL, male from Penang; g, USNM 148102, 695 mm TL, female from Persian Gulf, Saudi Arabia; h, MCZ 205, 763 mm TL, female from Singapore. Note: Figures e-h reduced twice that of Figures a-d.

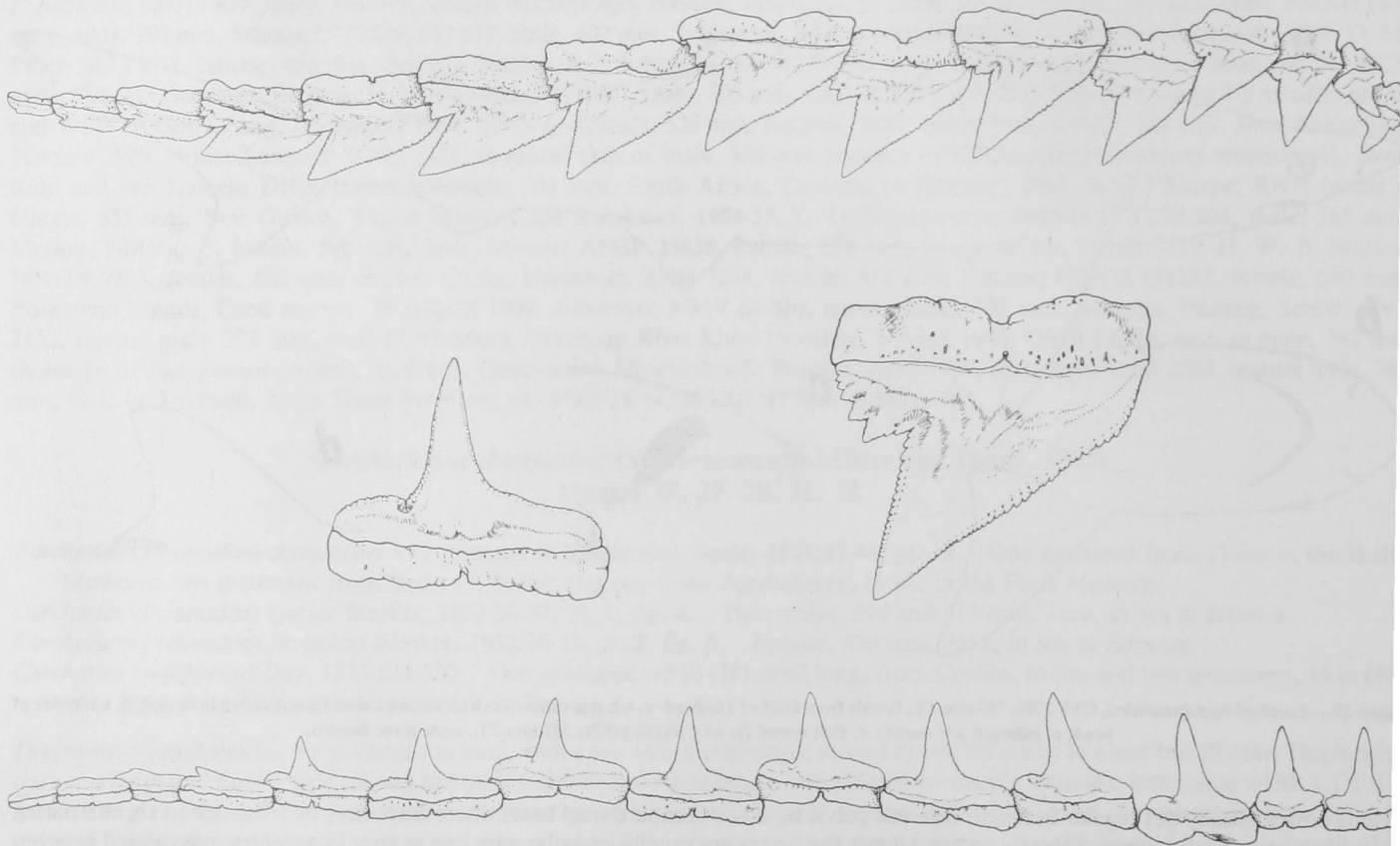


Figure 31.—*Carcharhinus dussumieri*, MCZ 205, 763 mm TL, female from Singapore: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

in *sealei*), the presence (*dussumieri*) or absence (*sealei*) of serrations on the enlarged lateral basal serrae of the upper teeth, and the two proportional dimensions given in Table 22.

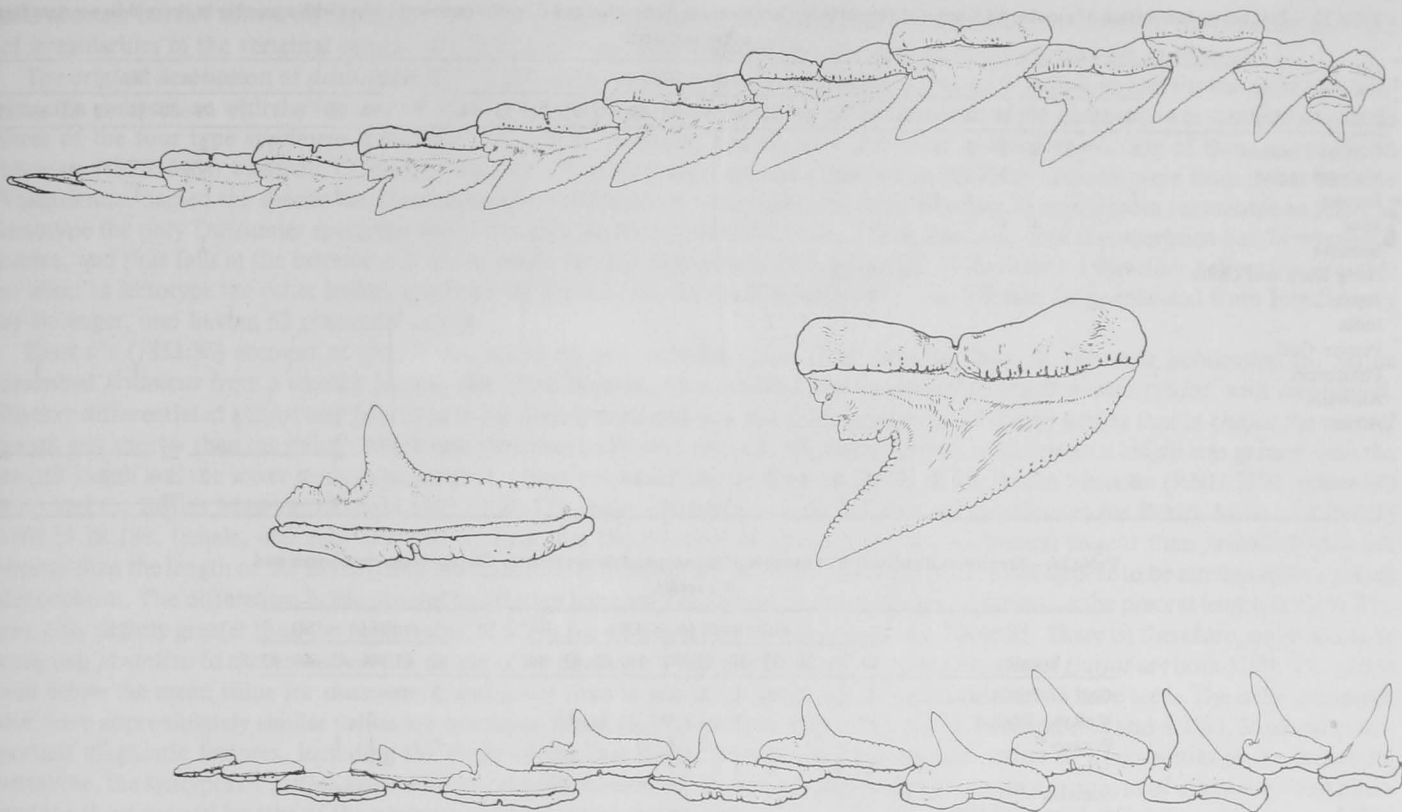


Figure 32.—*Carcharhinus dussumieri*, MCZ 109, 687 mm TL, male from Penang: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

Table 22.—Proportional dimensions showing differences between *Carcharhinus dussumieri* and *C. sealei* (n = number of specimens).

Species	Length anterior margin pectoral width pectoral			Width of mouth as % of TL		
	Range	Mean	n	Range	Mean	n
<i>dussumieri</i>	1.4-1.8	1.64	32	6.4-8.3	7.4	40
<i>sealei</i>	1.7-2.0	1.85	11	4.2-6.6	6.1	25

Nomenclatural discussion.—There is marked similarity between *dussumieri* and *sealei* (p. 48) in general external form, color including a black-tipped second dorsal fin, and the shape of the teeth. In consequence it is not surprising that earlier authors had difficulty in identifying their material. Adding to the problem, there is on the one hand the fact that these two species are sympatric throughout much of the Indo-Australian Archipelago, and on the other hand an indication from my material that in *dussumieri* there is variation apparently due to the existence of local populations or forms differing slightly from one another at the several island groups and regions throughout this species' range. This variation is manifest in some proportional dimensions, in snout shape, and in vertebral numbers. The development of locally recognizable populations of *dussumieri*, presumably due to partial isolation, is not too surprising in view of the relatively small size of these sharks and their inshore, shallow-water habitat. A consequence of the existence of these populations, and the factor of sexual dimorphism which affects the teeth and some proportional dimensions, is that examination of extreme morphological forms from different localities suggests that *dussumieri* includes more than one species—and seemingly this explains why earlier authors described the several nominal species here assigned to *dussumieri*. However, examination of a wider range of material shows sufficient variation within each population, and similarity between them, to negate this view.

Vertebral numbers, and particularly precaudal counts, provide the best means of distinguishing *dussumieri* and *sealei* (see Table 2). Although the precaudal counts for all of my material of these two species form a continuum with 54-74 for *dussumieri* and 74-85 for *sealei*, such a presentation masks the trenchant differences between the species in localities where they are sympatric, as evidenced by Table 23.

The wide range of precaudal numbers in *dussumieri* is due in part to extreme irregularity in the lengths of the centra at and behind the region where diplospondyly begins, and in part to great variability in the site of origin of diplospondyly which instead of being confined to the region above the pelvic base as is usual in most species of *Carcharhinus* can occur at any point from there to as far back as the second dorsal fin. Because of the latter situation, the numbers of monospondylous centra are also widely variable, and in fact such counts overlap with comparably made counts in *sealei* as shown in Table 24.

Reinforcing the differences between *dussumieri* and *sealei* shown by vertebral numbers are characteristic irregularities in the lengths of the centra which are discussed on p. 62 (*dussumieri*) and p. 53 (*sealei*) and which occur with sufficient frequency, especially in *dussumieri*, to be of considerable value.

Table 23.—Frequency distribution of number of precaudal vertebrae in *Carcharhinus dussumieri* and *C. sealei* (arrowed ranges with a number in the middle are data from other authors).

Locality	<i>dussumieri</i> (n = 43)																							<i>sealei</i> (n = 36)														
	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	74	75	76	77	78	79	80	81	82	83	84	85					
Gulf of Thailand	1		2	3	3	3	1																		1		2											
Malayan region					1										1	1									1	1												
Borneo	1					1	1			1													1		1				1									
Java			1	4	1	1																																
Sumatra																												1										
Hong Kong and China								4	2	2																												
Japan									1				1																									
India									1		1	1								1																		
Persian Gulf												1		1																								
Philippines																														1				1				
Australia																										1												
Africa																							1			1												
total	2		3	7	5	5	2	4	4	3	1	2	1	1	1	1						← 22 →		← 22 →		2	4	2	3		2			1				

Table 24.—Frequency distribution of number of monospondylous centra in *Carcharhinus dussumieri* and *C. sealei*.¹

Locality	<i>dussumieri</i> (n = 43)											<i>sealei</i> (n = 14)					
	34	35	36	37	38	39	40	41	42	43	44	42	43	44	45	46	47
Gulf of Thailand	1		2	5	1	3	1					2	1				
Malayan Region					1				1	1				2			
Borneo						2	1	1				1		1	1		
Java	1	1		3	2												
Sumatra															1		
Hong Kong and China				1	2		2	3									
Japan					2												
India				2	1						1						
Persian Gulf			1		1												
Philippines													1	1			
Australia																1	
Africa																2	
total	2	1	3	11	10	5	4	4	1	1	1	3	1	4	3		3

¹In this table monospondylous centra are those anterior to the first, short or diplospondylous centrum, even though long (monospondylous?) centra may also be present posterior to the site of diplospondyly.

The differences between the species in external morphology and in the nature of the teeth, as given in the respective diagnoses, are not always clear cut, and even the apparently obvious difference in the shape of the first dorsal fins is not as consistently useful as might be expected from comparison of Figures 23 and 24 with 28 and 29. Small specimens of *dussumieri*, like many other species, have more falcate first dorsal fins than do larger specimens, and hence such small specimens may resemble *sealei*. Differences in proportional dimensions show a great deal of overlap as is indicated in Table 25, and have limited value. The best of these differences relate to the length:width of the pectoral fin and to the width of the mouth, and data for these are shown graphically in Figure 33a, b.

The basis for referring the several nominal species to either *dussumieri* or *sealei* is displayed in part in Table 25. Other factors taken

Table 25.—Vertebral numbers and proportional dimensions used in referring

	Precaudal centra	Caudal centra	Monospondylous centra	Width mouth % TL
<i>Carcharhinus dussumieri</i>				
Data from present study excluding types	54-69 (60.1) n = 36	53-79 (63.7) n = 36	34-43 (38.3) n = 36	6.4-8.3 (7.4) n = 40
Data from types of nominal species here synonymized with <i>dussumieri</i>				
Syntypes of <i>Carcharias (Prionodon) dussumieri</i>	62-74 n = 2	68-76 n = 2	38-44 n = 2	7.6 n = 1
Syntypes of <i>Carcharias (Prionodon) tjutjot</i>	57 n = 2	71-72 n = 2	37-38 n = 2	7.2-7.7 n = 2
Holotype of <i>Carcharias (Prionodon) javanicus</i>	56	65	37	7.1
Syntypes of <i>Carcharias malabaricus</i>	64-65 n = 2	65 n = 1	37 n = 2	7.6 n = 1
<i>Carcharhinus sealei</i>				
Data from present study ¹ excluding types	74-85 (79.1) n = 35	73-83 (78.2) n = 13	42-47 (44.2) n = 13	4.2-6.6 (6.1) n = 25
Data from types of nominal species here synonymized with <i>sealei</i>				
Holotype of <i>Carcharias sealei</i> ²	—	—	—	6.6
Holotype of <i>Platyodon coatesi</i>	77	71	47	7.9

¹Including also information on the proportional dimensions of 12 specimens from Wheeler (1960—as *menisorrah*) and precaudal counts of 22

²Data extracted from Seale's (1910) illustration of *borneensis*

into account but not shown on the table were, of course, the shape of the first dorsal fin, the nature of the teeth, the presence and kind of irregularities in the vertebral centra, etc. Comments on those nominal species referred to *dussumieri* are as follows.

The original description of *dussumieri* by Valenciennes in Müller and Henle (1841:47) is scarcely definitive and for the most part consists of a comparison with the features of *sorrah*; the only illustration accompanying it is of one upper and one lower tooth. Fortunately three of the four type specimens mentioned are still in existence, and all are identifiable as *dussumieri*. One of these in the Berlin Museum (ISZZ 4464) was from China (no other locality data given), and the other two in the Paris Museum were from India. Because Valenciennes named the species for Dussumier who collected two of the syntypes from Bombay, it would seem reasonable to select as lectotype the only Dussumier specimen which can now be found (MNHN 1136). I find, however, that this specimen has 74 precaudal centra, and thus falls at the extreme end of the range for this character in all my material of *dussumieri*. I therefore believe it preferable to select as lectotype the other Indian specimen (MNHN 1135), an alcohol-preserved male, 370 mm long, collected from Pondicherry by Bélanger, and having 62 precaudal centra.

Bleeker's (1852:36) account of *tjutjot* was based on two subadult males from Batavia, Java. In the same publication (p. 38) he described *javanicus* from a smaller female, also from Batavia, Java, which I here synonymize, together with *tjutjot*, with *dussumieri*. Bleeker differentiated *tjutjot* and *javanicus* in his descriptions and in a key to his species (p. 28-29) by noting that in *tjutjot* the preoral length was shorter than the mouth length and the lower teeth were smooth, whereas in *javanicus* the preoral length was greater than the mouth length and the lower teeth were serrated. I have examined the syntypes of *tjutjot* in the Leiden Museum (RNH 7382, male, 580 mm) and the British Museum (BMNH 1867.11.28.177, male, 610 mm), and the holotype of *javanicus* in the British Museum (BMNH 1867.11.28.188, female, 466 mm) and can confirm that the syntypes of *tjutjot* have shorter preoral lengths than *javanicus* (but not shorter than the length of the mouth) and that there are differences in the teeth. The teeth differences appear to be attributable to sexual dimorphism. The differences in the preoral lengths are less easily explained. In the holotype of *javanicus* the preoral length is 7.2% TL, and only slightly greater than the mean value of 6.9% for 45 specimens of *dussumieri*, see Table 25. There is, therefore, no problem in assigning *javanicus* to *dussumieri* on this or any other character. The preoral lengths of the syntypes of *tjutjot* are both 5.8% TL, hence well below the mean value for *dussumieri*, and lower than in any other specimen of *dussumieri* that I have seen. The only specimens that have approximately similar values are one from Japan (6.1%) and two from the Gulf of Thailand (6.2 and 6.3%). In all other important diagnostic features, including the shape of the first dorsal fin and the presence and nature of irregularities in the precaudal vertebrae, the syntypes of *tjutjot* agree with *dussumieri*. In view of this agreement I accept *tjutjot* as a synonym of *dussumieri* and interpret the short preoral lengths of the syntypes as representing one extreme of the variation in this feature. I designate as lectotype of *tjutjot* the Leiden Museum specimen (RNH 7382), a male of 580 mm TL from Batavia, which was the first of the two listed by Bleeker in his original description.

The species name *javanicus* was earlier used by Van Hasselt (1823:315) in the binomen *Carcharias Javanicus*. A French translation of Van Hasselt's account appeared in 1824. Van Hasselt's usage was in a letter to the director of the Leiden Museum, C. J. Temminck, as follows: "Mijn *Carcharias Javanicus*, komt het meest nabij aan *Meni Sauru*, die zich in het Museum te Parijs bevindt, van welken hij echter in den vorm der Pinna Caud. verschilt." M. Boesman of the Leiden Museum, who kindly supplied me with information on Van Hasselt, also provided a translation of the above passage: "My *Carcharias Javanicus*, is most close to *Meni Sauru*, which is present in the Museum of Paris, from which, however, it differs in the shape of the Pinna Caud."

The above account has been regarded by some authors as constituting a description of *Carcharias javanicus* Van Hasselt, 1823, since it refers to the shape of the caudal fin. If this argument is accepted, there still remains the problem of identifying the species. Even if one assumes, as did Férussac (Van Hasselt 1824:89), that Van Hasselt's *Meni Sauru* is "*Meni Sorra* (*C. sorra* Cuv.) du musée de Paris," this does not appreciably assist in identifying even the species which Van Hasselt used for comparison with his *javanicus*. The specific names *menisorrah* and *sorrah* did not become available until 1841 as *Carcharias (Prionodon) menisorrah* Valenciennes in Müller and Henle and *Carcharias (Prionodon) sorrah* Valenciennes in Müller and Henle. The comparison was therefore made on vernacular names. A study of what specimens were available in the Paris Museum in 1823 and earlier might yield evidence as to the identity of *Meni Sauru*, but would still leave open the question of the identity of *javanicus* Van Hasselt because this author did not state the man-

various nominal species to either *Carcharhinus dussumieri* or *C. sealei*.

1st dorsal base % TL	1st dorsal base 1st dorsal height	Snout tip to 1st gill opening % TL	Internarial distance % TL	Prenarial length % TL	Preoral length % TL	Length anterior margin of pectoral width pectoral
8.8-11.2 (9.9) <i>n</i> = 40	0.94-1.41 (1.08) <i>n</i> = 39	15.4-19.4 (17.4) <i>n</i> = 26	4.3-5.5 (4.9) <i>n</i> = 40	2.7-4.0 (3.3) <i>n</i> = 40	6.1-8.4 (6.9) <i>n</i> = 40	1.4-1.8 (1.64) <i>n</i> = 27
9.0 <i>n</i> = 1	0.87 <i>n</i> = 1	18.9 <i>n</i> = 1	5.2 <i>n</i> = 1	3.2 <i>n</i> = 1	6.7 <i>n</i> = 1	1.7 <i>n</i> = 1
9.5-9.6 <i>n</i> = 2	0.98-1.01 <i>n</i> = 2	16.4 <i>n</i> = 1	4.2-4.3 <i>n</i> = 2	3.0 <i>n</i> = 2	5.8 <i>n</i> = 2	1.6-1.7 <i>n</i> = 2
9.6	0.90	18.7	5.0	3.4	7.2	1.7
9.0 <i>n</i> = 1	0.96 <i>n</i> = 1	18.8 <i>n</i> = 1	4.9 <i>n</i> = 1	3.5 <i>n</i> = 1	7.5 <i>n</i> = 1	1.6 <i>n</i> = 1
7.6-9.4 (8.8) <i>n</i> = 26	0.78-1.06 (0.92) <i>n</i> = 25	14.4-17.3 (15.8) <i>n</i> = 25	3.8-5.2 (4.4) <i>n</i> = 25	2.2-3.7 (3.0) <i>n</i> = 25	5.3-7.3 (6.5) <i>n</i> = 25	1.7-2.0 (1.85) <i>n</i> = 11
8.8	1.00	17.8	4.4	3.6	6.7	2.0
9.7	0.99	16.8	4.6	2.4	5.5	—

specimens from Bass et al. (1973).

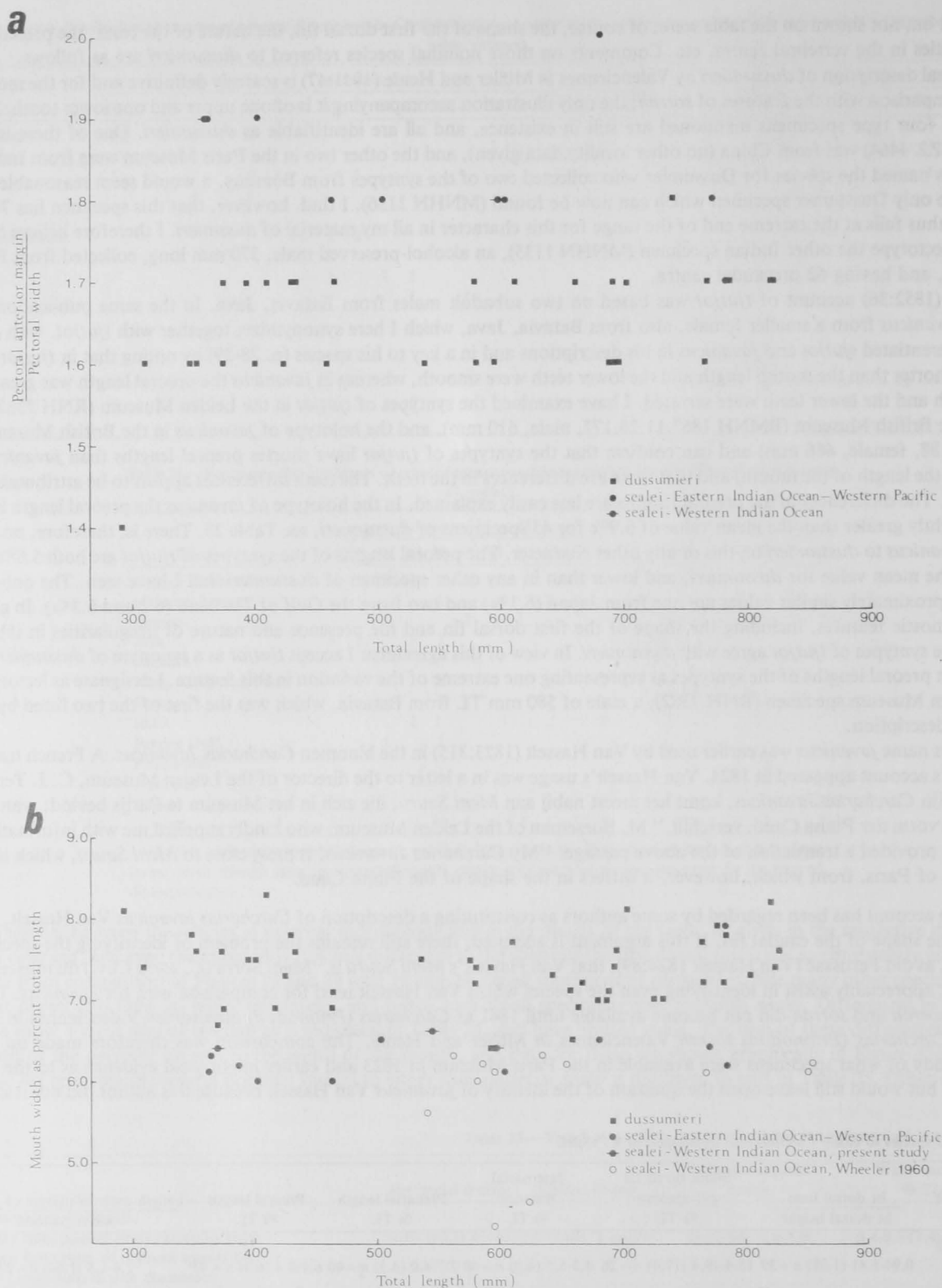


Figure 33.—Proportional dimensions indicating differences between *Carcharhinus dussumieri* and *C. sealei*: a, pectoral fin anterior margin divided by pectoral fin width versus total length; b, mouth width as percent of total length versus total length.

ner in which the caudal fin of his species differed from that of *Meni Sauru*. In the absence of other evidence, and of type material, I see no way of adopting *Carcharias javanicus* Van Hasselt, and hence relegate it to the category of nomen dubium.

Day (1873:529) described *malabaricus* from three specimens from the west coast of India. The account was not illustrated and is inadequate for determining the species. Two of the syntypes are still in evidence, one at the British Museum (BMNH 89.2.1.4173, male, 375 mm) from Cochin, the other at the Australian Museum (AMS I.61, female, 422 mm) from Calicut. Both syntypes clearly fit *dussumieri*. I designate the British Museum specimen, data for which are given in Tables 25 and 26, as lectotype of *malabaricus* since it was the first of the three listed by Day in his original account.

Table 26.—*Carcharhinus dussumieri*, proportional dimensions in percentage of total length.

	♀ 310 mm Java Batavia MCZ 1386	♂ 375 mm Hong Kong USNM 6457	¹ ♂ 375 mm India Cochin BMNH 89. 2.1.4173	² ♂ 435 mm India Bombay MNHN 1136	³ ♀ 466 mm Java Batavia BMNH 1867. 11.28.188	♀ 580 mm Japan Nagasaki UMMZ 177114	⁴ ♂ 580 mm Java Batavia RNH 7382	♀ 695 mm Persian Gulf Saudi Arabia USNM 148102	♀ 763 mm Singapore MCZ 205	♀ 825 mm Gulf of Thailand GVF 2132
Snout tip to										
outer nostrils	3.4	3.7	3.5	3.2	3.4	3.7	3.0	3.6	3.5	2.9
eye	7.4	7.2	7.2	6.6	7.0	7.1	5.8	6.9	6.9	6.1
mouth	7.9	7.7	7.5	6.7	7.2	7.1	5.8	7.4	6.9	6.4
1st gill opening	19.0	17.3	18.8	18.9	18.7	17.5	16.4	18.4	18.5	15.4
3d gill opening	21.3	19.7	21.5	21.2	20.6	—	—	20.6	20.4	18.4
5th gill opening	23.5	21.6	23.2	23.9	22.7	22.0	19.8	22.0	22.9	20.6
pectoral origin	22.2	20.8	22.7	23.0	22.1	20.9	19.7	20.9	21.8	20.0
pelvic origin	46.3	46.7	47.9	45.7	46.0	46.1	45.3	47.5	48.2	50.1
1st dorsal origin	29.3	29.9	31.2	29.7	29.7	28.4	29.3	30.6	31.1	30.9
2d dorsal origin	61.9	60.6	61.0	60.3	60.2	62.1	61.0	62.7	64.9	64.5
anal fin origin	60.4	60.0	61.0	59.4	59.3	60.0	60.8	60.7	63.7	63.3
upper caudal origin	73.9	72.3	72.8	73.2	73.8	74.7	74.1	75.7	76.4	76.1
lower caudal origin	72.7	71.5	71.7	72.2	72.9	73.8	73.0	74.7	75.5	75.4
Nostrils										
distance between inner corners	5.5	5.2	4.9	5.2	5.0	4.9	4.2	4.5	5.0	4.8
Mouth										
width	7.4	6.9	7.6	7.6	7.1	7.4	7.2	7.6	7.7	7.6
length	4.7	4.5	4.8	4.9	4.6	4.4	5.2	4.5	4.6	3.9
Labial furrow lengths										
upper	0.5	0.4	0.4	0.5	0.4	0.4	0.3	0.4	0.5	0.3
lower	0.3	0.3	0.4	0.5	0.2	0.5	0.3	0.4	0.4	0.3
Gill opening lengths										
1st	2.3	2.1	—	—	2.5	2.4	2.4	2.6	2.9	3.0
3d	2.6	2.4	2.5	3.3	2.7	2.8	3.5	3.2	3.5	3.5
5th	1.6	1.9	—	—	2.5	2.2	2.8	2.3	2.8	2.4
Eye										
horizontal diameter	2.7	2.7	2.5	2.6	2.6	2.2	2.2	2.0	2.0	2.0
1st dorsal fin										
length of base	10.8	10.7	9.0	9.0	9.6	10.0	9.5	10.9	10.5	10.2
length posterior margin	3.9	4.0	4.5	4.8	4.5	4.3	4.6	4.3	4.3	3.8
height	8.7	8.0	9.5	10.3	10.7	9.3	9.7	9.3	10.7	9.3
2d dorsal fin										
length of base	4.4	4.0	3.7	4.1	4.6	4.3	4.1	4.7	4.1	4.7
length posterior margin	3.9	4.0	4.3	4.1	3.2	4.1	4.5	3.7	4.1	3.5
height	2.9	3.1	3.2	3.2	3.4	2.9	3.5	3.4	3.7	3.0
Anal fin										
length of base	5.2	4.8	4.4	4.9	5.1	5.6	4.6	5.3	4.5	5.0
length posterior margin	3.4	3.7	4.0	3.9	3.6	3.4	3.9	4.1	3.9	3.2
height	3.4	3.7	3.5	3.9	4.1	3.6	3.7	3.7	4.2	3.6
Pectoral fin										
length of base	5.5	6.1	5.8	5.3	5.6	5.9	5.8	6.5	6.4	5.9
length anterior margin	14.5	15.7	16.0	15.9	15.4	14.8	15.2	17.1	17.2	15.6
length distal margin	10.5	10.4	11.1	11.3	10.5	10.3	11.4	12.6	13.9	12.4
greatest width	8.9	9.3	9.7	9.4	9.2	9.1	9.5	10.7	10.9	9.4
Pelvic fin										
length of base	5.3	4.8	4.5	5.0	5.1	5.2	5.0	5.6	6.6	5.2
length anterior margin	6.1	5.9	5.6	6.2	6.4	6.6	6.9	6.8	6.5	5.8
length distal margin	5.5	5.1	5.3	5.0	5.3	4.8	5.1	6.0	6.4	5.9
length of claspers	—	2.0	2.7	2.2	—	—	4.5	—	—	—
Caudal										
length of upper lobe	25.1	27.7	26.9	27.3	25.8	25.4	25.8	24.6	24.0	24.1
length of lower lobe	9.8	10.4	10.4	10.7	12.0	10.3	11.2	10.5	11.8	10.8
Trunk at pectoral origin										
width	10.9	10.9	10.9	11.3	10.7	10.7	9.8	12.1	13.1	12.2
height	10.1	10.9	9.1	10.1	10.7	10.9	9.6	10.9	11.3	11.7
Dental formula	$\frac{12-2-12}{13-1-13}$	$\frac{13-1-13}{13-1-13}$	—	$\frac{13-2-14}{12-2-12}$	$\frac{14-2-13}{14-1-14}$	$\frac{13-2-13}{14-1-14}$	$\frac{13-2-13}{13-1-13}$	$\frac{14-2-13}{14-2-14}$	$\frac{13-2-13}{13-13}$	$\frac{12-2-12}{13-1-13}$
Vertebrae										
precaudal	57	61	65	74	56	62	57	67	69	56
caudal	61	67	65	76	65	61	71	65	70	54
total	118	128	130	150	121	123	128	132	139	110

¹Syntype of *Carcharias malabaricus*.²Syntype of *Carcharias (Prionodon) dussumieri*.³Holotype of *Carcharias (Prionodon) javanicus*.⁴Syntype of *Carcharias (Prionodon) tjutjot*.

Some measure of the confusion in the literature over the status of the nominal species here placed in *dussumieri* or in *sealei* is provided by Day's subsequent treatment of his *malabaricus* and other related species. In his monograph of the fishes of India (Day 1878:716), he relegated *malabaricus* to the synonymy of *menisorrah*, in which he also placed *tjutjot* Bleeker. He referred to a specimen of *menisorrah* which he had received from Bleeker. The *menisorrah* of Bleeker, judging by museum specimens that I have seen and literature accounts, is usually, but not in every case, referable to *dussumieri*. Day's *menisorrah* likewise fits *dussumieri* if his (1878, pl. 184, fig. 1) illustration of a Kozhikode specimen is taken as a criterion. Day was, therefore, correct in synonymizing *malabaricus* and *tjutjot* with what he called *menisorrah* but which should have been called *dussumieri*. In the same monograph Day treated (p. 714) a second species under the name *dussumieri*. This species, judging by Day's illustration (pl. 187, fig. 2) of a specimen from Malabar, appears to be *sealei*. Day placed *javanicus* Bleeker in its synonymy, and hence was nomenclaturally correct in referring *javanicus* to *dussumieri* but taxonomically incorrect in recognizing as *dussumieri* the species which at that time did not have a valid name and subsequently was named *sealei*.

The foregoing example of confusion in the literature is by no means an isolated case with respect to the names *dussumieri*, *menisorrah*, etc. The consequence is that very few of the numerous literature identifications under these names can be taken at face value, particularly if they are mere listings and not accompanied by illustrations.

Description (see also Table 26).—Small sharks, growing to about 1 m TL. Midline of back between dorsal fins with a low dermal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles close-packed, only slightly overlapping in small specimens but more regularly overlapping in larger, subcircular to ovoid in outline, each with three longitudinal ridges and corresponding posterior marginal teeth in small specimens but with five ridges and teeth in larger specimens.

Snout of moderate length, varying from pointed to sharply rounded in contour. Anterior margin of eye above or slightly forward of front of mouth. Nostrils oblique, with broadly ovate apertures, the anterior margin of each with a well-developed, sharply pointed lobe.

Dental formula $\frac{13-1 \text{ to } 3-13}{14-0 \text{ to } 2-14}$ in 12 of 39 specimens counted; $\frac{13-1 \text{ or } 2-13}{13-1-13}$ in 9; $\frac{12 \text{ or } 13-2-12 \text{ or } 13}{12 \text{ or } 13-0 \text{ or } 1-12 \text{ or } 13}$ in 8

$\frac{12 \text{ or } 13-0 \text{ or } 2-12 \text{ or } 13}{13 \text{ or } 14-1-13 \text{ or } 14}$ in 5; $\frac{13 \text{ or } 14-2-13 \text{ or } 14}{11 \text{ to } 14-1 \text{ or } 2-12 \text{ to } 14}$ in 4; and $\frac{13-2-13}{15-1-15}$ in 1. Teeth sexually dimorphic in adult specimens. Upper teeth of females and immature males moderately broad, oblique, their lateral margins deeply notched, their medial margins convex basally but straight or weakly concave distally; several large serrae basally on the lateral margin of each tooth; medial and lateral margins of upper teeth, including the lateral basal serrae, regularly serrated, the serrations rather coarse; upper teeth of mature males much narrower than those of females, more oblique and more finely serrated; one, two (exceptionally three or none) smaller symphysial teeth, not always well differentiated from the paramedian teeth in either size or shape and hence somewhat arbitrarily designated. Lower teeth narrower than the upper, those of females and immature males only slightly oblique, their lateral margins notched, their medial margins concave, usually both margins serrated, the serrations finer than those of upper teeth, though sometimes there are larger irregular serrae or crenulations basally on the lateral margins; in mature males the first four or five series of paramedian lower teeth are considerably more oblique than those of females, and are essentially smooth edged except for some fine basal serrations; usually one smaller symphysial tooth but occasionally two or none.

First dorsal fin moderately high, weakly falcate in small specimens (where a vertical from its apex falls not farther back than midway along its rear tip) but more erect in larger specimens where its apex is vertically above or in front of its axil; origin of first dorsal over or slightly behind the middle of the inner (posterior) margin of the pectoral fin in small specimens but further rearward to almost over the inner (posterior) corner in larger specimens. Second dorsal fin of moderate size, almost equal to anal fin; length of second dorsal rear tip 0.96-1.50 (mean 1.27) times second dorsal height in 33 specimens; origin of second dorsal above or usually slightly behind anal fin; origin to as far back as anterior one-third of anal base. Pectoral fins moderately short, falcate, with pointed tips; origin of pectorals below the fourth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches from two-thirds along first dorsal base almost to first dorsal axil.

Color after preservation in alcohol is grayish or brownish above, paler below; all fins except the second dorsal are at most only slightly darker than the upper trunk color, and have pale trailing edges probably whitish or translucent in life; second dorsal fin dusky to black on its apical two-thirds but pale to white along its rear tip and just in front of the axil.

Vertebral counts of 10 specimens are given in Table 26 and of another 33 specimens in Table 27.

Centrum diameter greater than centrum length except for the last few monospondylous centra which range from moderately to greatly elongated. In 39 of the 43 specimens for which I have radiographs there is obvious and often considerable irregularity in the length of the centra between the pelvic base and the second dorsal base. The irregularity involves the alternation of long and short centra with lengths corresponding to monospondylous and diplospondylous centra, respectively. The alternations themselves are usually serially regular, with from one to six alternating pairs of centra present, but in some cases there are one or two alternating pairs followed by two or three long centra before the next short centrum. The four specimens lacking these irregularities are from the Gulf of Thailand, Malaya, and Borneo. Localities for the 39 specimens which have irregularities are the Gulf of Thailand, Hong Kong, China, Japan, India, the Persian Gulf, the Malayan region, Borneo, and Java. For the purpose of this account, diplospondyly is regarded as occurring at the first short centrum, even though long (monospondylous?) centra may be present posteriorly. On this basis the site of diplospondyly is variable, ranging in position from over the pelvic base to beneath the second dorsal base. Between the second dorsal base and the caudal origin the centra are mostly short (i.e., clearly diplospondylous) and regular or nearly so. Posterior to the caudal origin, on the caudal axis, there is further irregularity in centrum length in 29 of the 43 specimens examined. This caudal irregularity

Table 27.—Vertebral numbers in 33 specimens of *Carcharhinus dussumieri*.

Specimens		Precaudal	Caudal	Total
GVF 1548	Gulf of Thailand	54	65	119
GVF 2469	Gulf of Thailand	56	53	109
GVF 2385	Gulf of Thailand	57	58	115
GVF 2415	Gulf of Thailand	57	63	120
GVF 2454	Gulf of Thailand	57	67	124
GVF 2568	Gulf of Thailand	58	62	120
GVF 2383	Gulf of Thailand	58	64	122
GVF 2415	Gulf of Thailand	58	66	124
GVF 2460	Gulf of Thailand	59	61	120
GVF 2568	Gulf of Thailand	59	63	122
GVF 2415	Gulf of Thailand	59	66	125
GVF 2409	Gulf of Thailand	60	65	125
SU 27726	Borneo	54	70	124
CNHM 21878	Borneo	59	68	127
USNM 197386	Borneo	60	69	129
USNM 197386	Borneo	63	65	128
USNM 72478	Java	57	64	121
BMNH 1867.				
11.28.177	Java ¹	57	72	129
USNM 72477	Java	58	61	119
USNM 177112	Java	59	65	124
MCZ 109	Malaya, Penang	58	71	129
MCZ 110	Malaya, Penang	68	79	147
SU 31254	Hong Kong	61	58	119
SU 31254	Hong Kong	61	60	121
ANSP 52650	Hong Kong	61	61	122
ANSP 76545	Hong Kong	62	62	124
ANSP 52651	Hong Kong	62	63	125
SU 14113	China, Chusan Island	63	60	123
ANSP 76859	Hong Kong	63	65	128
MNHN 1135	India, Pondicherry ²	62	68	130
AMS I.61	India, Calicut ³	64	—	—
UZMK PO 692	Persian Gulf	65	66	131
UMMZ 179015	Japan	66	60	126
Range (including counts from Table 26)		54-74	53-79	109-150

¹Syntype of *Carcharias (Prionodon) tjtjtjt*.²Syntype of *Carcharias (Prionodon) dussumieri*.³Syntype of *Carcharias malabaricus*.Table 28.—Clasper length as percentage of total length in *Carcharhinus dussumieri*.

TL (mm)	Clasper length as % TL	Locality
353	2.8	Borneo
375	2.0	Hong Kong
400	2.0	Gulf of Thailand
577	2.3	Gulf of Thailand
580	4.5	Java
594	2.0	Java
610	5.1	Java
660	2.3	Java
687	8.9	Malaya, Penang
688	3.6	Gulf of Thailand
703	9.5	Borneo
726	8.0	Gulf of Thailand
738	7.2	Gulf of Thailand

¹Syntype of *Carcharias (Prionodon) tjtjtjt*.

varies from slight to extreme and involves the presence of one to four or more elongated centra interposed amongst the shorter centra. There is no uniformity in the position of the elongated centra nor usually in their length which may be up to three times that of the adjacent short centra. It is evident that most of these long centra are the result of fusions, as they carry two or three haemal rays while the short centra each carry only one. Specimens not showing irregularities on the caudal axis are from the Gulf of Thailand (1 out of 13), India (4 of 4), Persian Gulf (2 of 2), the Malayan region (2 of 3), Borneo (3 of 4), and Java (2 of 7). Specimens showing irregularities are from the Gulf of Thailand, Hong Kong, China, Japan, the Malayan region, Borneo, and Java. There is no obvious correlation between the presence and extent of these irregularities on the caudal axis and those further anterior in the precaudal diplospondylous region. The

$\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 1.10-1.73 (mean 1.48) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$

was 1.23-3.28 (mean 2.45) in 43 specimens.

The smallest, apparently free-living specimen I have seen was 310 mm TL, while the largest embryo was 392 mm. Teshima and Mizue (1972) reported embryos up to 373 mm from off northwest Borneo; their smallest free-living specimen was 380 mm. Blegvad (1944) listed an embryo of 300 mm from the Persian Gulf. Male specimens that I have measured had clasper lengths as shown in Table 28, indicating that maturity is reached at a total length of about 650-700 mm.

I have found no data in the literature on the size at which females become mature, but it could be expected to be comparable to or somewhat greater than in the males, and hence in the order of 700-750 mm TL. Teshima and Mizue (1972) noted that there were usually two embryos per litter in their Borneo material, and that gravid females taken in July contained embryos from 25 to 373 mm long; they concluded from their data that there was no seasonality in reproduction except that pupping was more frequent in July and August. They further supported their conclusions with data from Yang⁷ that gravid females in the South China Sea "...are, on an average, caught every month, especially from February to March and July to August. The usual number of embryos contained in each uterus is 1, in rare cases, 2 embryos are found in each uterus." Blegvad (1944) recorded a female with a litter of four embryos from the Persian Gulf. The largest specimens that I have seen were a male of 823 mm TL from Japan and a female of 825 mm from the Gulf of Thailand. Blegvad (1944) stated that of 562 specimens listed from the Persian Gulf "hardly anyone was more than 1 m long."

⁷Teshima and Mizue (1972:229) reported these data as a personal communication from Yang of the Taiwan Fisheries Research Institute.

Distribution (see also Material examined).—Based on specimens I have examined, *dussumieri* occurs in shallow coastal waters from the Persian Gulf eastwards to China and Japan, and southwards through the Indo-Australian Archipelago to Java. Blegvad (1944, as *menisorrah*) reported that it was the most common shark in the Persian Gulf. His illustration (fig. 10) of a specimen showing an erect (not falcate) first dorsal fin plus the black-tipped second dorsal fin is sufficient to confirm the identification of his material as *dussumieri*, but in addition I have seen one of his specimens, and also another from the Persian Gulf. In Indian waters *dussumieri* is present on both coasts, from Bombay in the northwest to at least Pondicherry in the southeast. It apparently is common in the Gulf of Thailand, and extends northeastwards to Hong Kong and the China coast to at least as far north as Chusan Island, and to Japan as far as Nagasaki. Chen (1963) illustrated it, as *menisorrah*, from the Pescadores, and reported it from Taiwan. Confirmed records in the Indo-Australian Archipelago are from Malaya (Penang), Singapore, Borneo, and Java, but it is unlikely that *dussumieri* is restricted to these localities. However, because of the very close similarity between *dussumieri* and *sealei*, unusual care will need to be taken in the identification of specimens which would extend the present range.

Material examined.—RNH 7384, four females, 243 to ca. 690 mm, and two males, 287 and 596 mm, Bleeker; ZSZM (—), three embryos, two males, 245 and 260 mm, and one female, 247 mm, China, Fo-Kien Province, 1904, G. Siemsson; ZSZM (—), two embryos, male, 265 mm, and female, 332 mm, China, Fo-Kien Province, 8 September 1911, G. Siemsson; UZMK PO.692, female embryo, 29 mm, Persian Gulf, Udfor Kangun, 9 February 1938, H. Blegvad; SU 31254, female embryo, 300 mm, and male, 304 mm, Hong Kong, A. W. Herre; MCZ 1386, female, 310 mm, Java, Batavia, O. Bryant and W. Palmer; MSNG C.E. 23319, female, 315 mm, Borneo, 1886; ISZZ 20233, female, 320 mm, "Japan and Formosa," Haberer; SU 27726, male, 348 mm, Borneo, Sandakan, A. W. Herre; CNHM 21878, male, 353 mm, Borneo, Sandakan, 2 July 1929, A. W. Herre; BMNH 1928.4.24.2, embryo, 363 mm, China, Chefoo; MNHN 1135, male, 370 mm [syntype of *Carcharias (Prionodon) dussumieri*], India, Pondicherry, Bélanger; GVF 2568, two females, 372 and 418 mm, Gulf of Thailand, Prachuap Khiri Khan Province, ca. 11°25' to 11°45'30"N, 99°43' to 99°53'E, 6-11 May 1961; USNM 6457, male embryo, 375 mm, Hong Kong, W. Stimpson; BMNH 89.2.1.4173, male, 375 mm (syntype of *Carcharias malabaricus*), India, Cochin, F. Day; BMNH 1939.1.17.1-2, two embryos, male, 388 mm, and female, 392 mm, Hong Kong, Herklots; NMV 61-361 and 61-425, male, 390 mm, and female, 545 mm, Java, 1857-59, *Novara*; GVF 1548, female, 397 mm, Gulf of Thailand, Chon Buri Province, off Chon Buri City, 7-9 December 1957; GVF 2409, male, 400 mm, Gulf of Thailand, Prachuap Khiri Khan Province, ca. 33 mi offshore ESE of Kau Sarmroi-yord, 26-29 August 1960; UZMK PO 686, female, 402 mm, Japan, Nagasaki, 1911, D. S. Jordan; MCZ 110, female, 410 mm, Malaya, Penang, 20 August 1860, Putnam; ZSZM 1197, female, 412 mm, Java; AMS 1.61, female, 422 mm (syntype of *Carcharias malabaricus*), India, Calicut, F. Day; SU 7928, female, 424 mm, and male, 465 mm, Japan, Nagasaki, D. S. Jordan and J. O. Snyder; GVF 2385, two females, 431 and 777 mm, Gulf of Thailand, Prachuap Khiri Khan Province, ca. 20 mi offshore ESE of Kau Sarmroi-yord, 17-21 August 1960; MNHN 1136, male, 435 mm [syntype of *Carcharias (Prionodon) dussumieri*], India, Bombay, Dussumier; NMV (—), male, 455 mm, Hong Kong; BMNH 1867.11.28.188, female, 466 mm [holotype of *Carcharias (Prionodon) javanicus*], Java, Batavia, P. Bleeker; ISZZ 4464, female, 492 mm [syntype of *Carcharias (Prionodon) dussumieri*], China, Meyen; NMV (—), male, 515 mm, Borneo, 1897; SU 14113, female, 517 mm, China, Chusan Island, Tinghai, October 1936, A. W. Herre; GVF 2469, female, 538 mm, Gulf of Thailand, about 50 mi offshore E of Prachuap Khiri Khan town, 10-16 January 1961; GVF 2454, male, 577 mm, Gulf of Thailand, Rayong Province, 28 mi SSE of Goh Chung, 28 December 1960-2 January 1961; UMMZ 177114, female, 580 mm, Japan, East China Sea, Nagasaki, 15 July 1929, C. L. Hubbs; RNH 7382, male, 580 mm [syntype of *Carcharias (Prionodon) tjutjot*], Java, Batavia, P. Bleeker; USNM 72477, female, 594 mm, Java, Batavia, 1909, O. Bryant and W. Palmer; USNM 72478, female, 595 mm, Java, Batavia, 1909, O. Bryant and W. Palmer; BMNH 1867.11.28.177, male, 610 mm [syntype of *Carcharias (Prionodon) tjutjot*], Java, Batavia, P. Bleeker; RNH 7375, male, 635 mm, Indian Archipelago, 1852, P. Bleeker; GVF 2415, two females, 643 and 658 mm, and male, 688 mm, Gulf of Thailand, Prachuap Khiri Khan Province, about 24 mi offshore ENE of Kau Sarmroi-yord, 26 August-1 September 1960; UMMZ 177112, male, 660 mm, Java, near Batavia, 6-15 May 1929, J. D. F. Hardenberg and C. L. Hubbs; GVF 1565, female, 665 mm, Gulf of Thailand, Rayong Province, Rayong Bay, 12°30' to 12°40'N, 101°00' to 101°25'E, 11-17 December 1957; GVF 1541, female, 667 mm, Gulf of Thailand, between Chon Buri and Rayong, 6-7 January 1961; MCZ 109, mature male, 687 mm, Malaya, Penang, 20 August 1860, Putnam; USNM 197386, female, 693 mm, and mature male, 703 mm, Sulu Sea near North Borneo (via Manila Fish Market), March 1962, V. G. Springer; USNM 148102, female, 69 mm, Persian Gulf, Saudi Arabia, Tarut Bay, Zaal Island, 15 May 1948, D. S. Erdman; GVF 1565, mature male, 726 mm, Gulf of Thailand, Rayong Province, Rayong Bay, 12°30' to 12°40'N, 101°00' to 101°25'E, 11-17 December 1957; GVF 2383, mature male, 738 mm, and female, 803 mm, Gulf of Thailand, Trat Province, about 10 mi E of south tip of Goh Kut, 15-20 August 1960; GVF 2460, female, 766 mm, Gulf of Thailand, Rayong Province, 15-28 mi offshore SE of Goh Chuang, 2-8 January 1961; MCZ 205, female, 76 mm, Singapore, 1859, Putnam; GVF 2563, female, 781 mm, Gulf of Thailand, Surat Thani Province, about 5 mi offshore E of Goh Samui, 6-8 May 1961; GVF 2706, female, 785 mm, Gulf of Thailand, 38 mi from Ko Chang, 11°37.1'N, 101°46.6'E, 22-23 November 1960, MV *Stranger*; ISH TFS 77/61, female, 795 mm, Gulf of Thailand, 10 August 1961; GVF 2699, female, 812 mm, Gulf of Thailand, 40.1 mi from Paulo Paujang, 8°57.0'N, 102°53.3'E, 15 November 1960, MV *Stranger*; UMMZ 179015, mature male, 82 mm, Japan, supposedly from East China Sea, via Osaka Market, 10 July 1929, C. L. Hubbs; GVF 2132, female, 825 mm, Gulf of Thailand, Prachuap Khiri Khan Province, 5 April 1960; ANSP 76545, one specimen, Hong Kong; ANSP 76549, one specimen, Hong Kong; ANSP 52650-52651, two specimens, Hong Kong.

Carcharhinus acronotus (Poey, 1860)
 Figures 34, 35

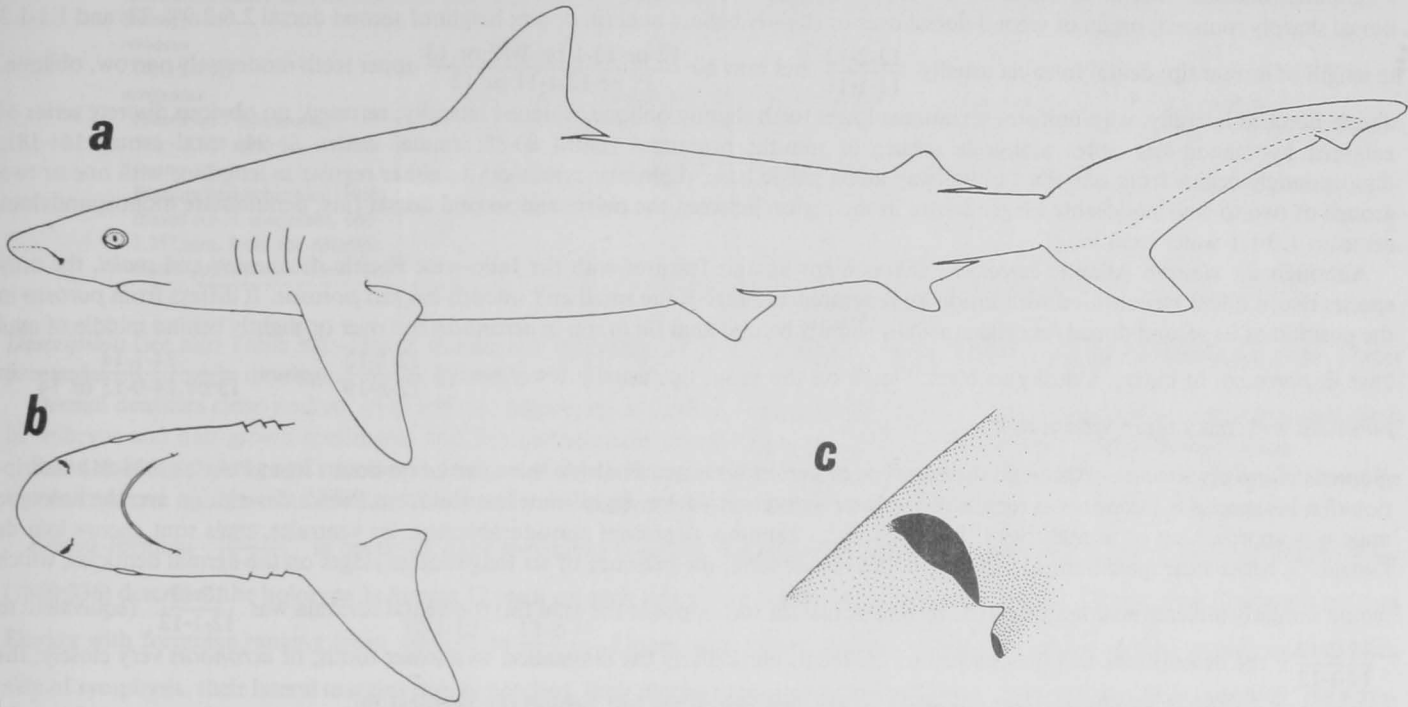


Figure 34.—*Carcharhinus acronotus*, UPR (—), 1,004 mm TL, female from Puerto Rico: a, left side; b, underside of head; c, enlarged left nostril.

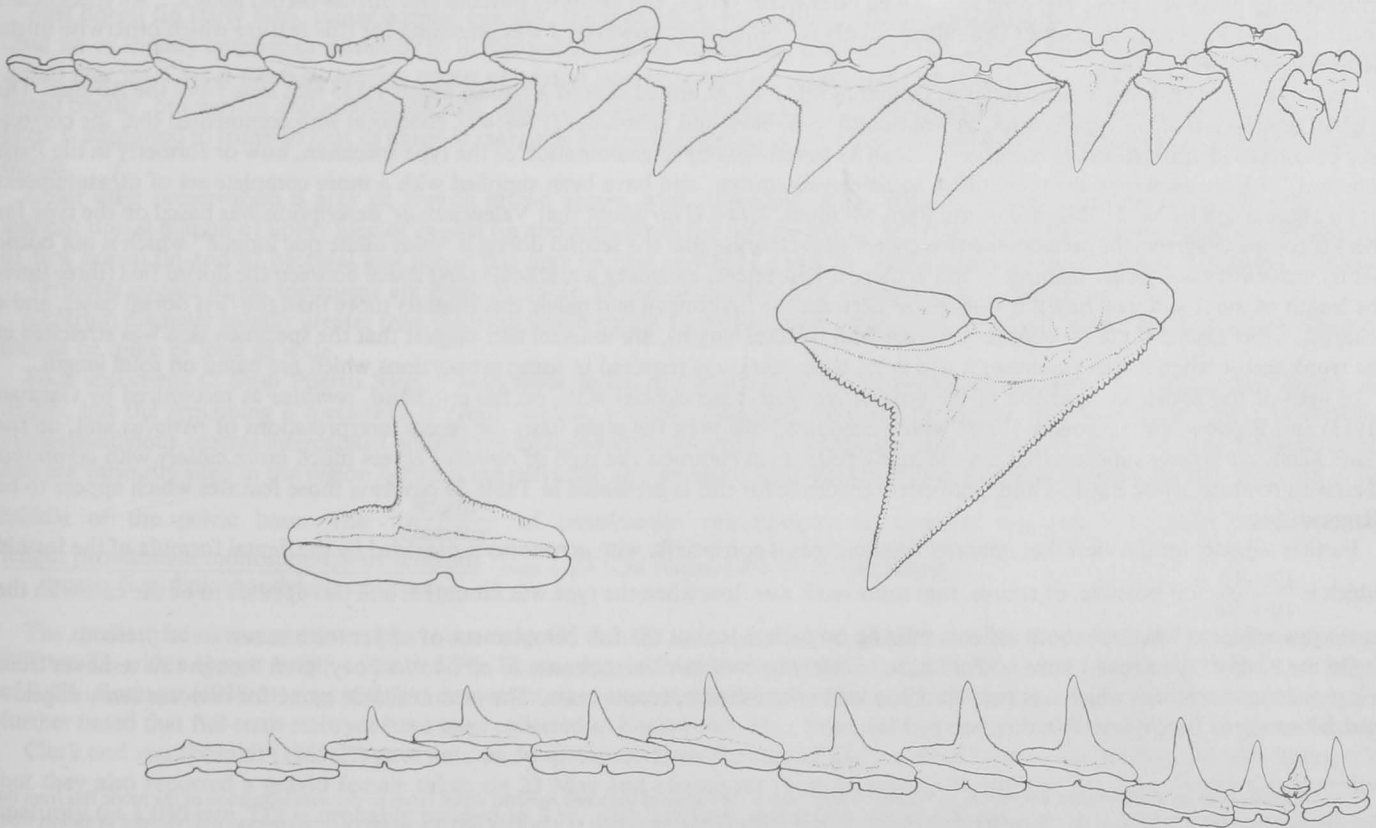


Figure 35.—*Carcharhinus acronotus*, USNM 126115, 1,064 mm TL, male from Florida: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

Squalus acronotus Poey, 1860:335-336, pl. 19, figs. 3, 4. Male, 980 mm, Cuba.

Carcharias (Prionodon) remotus Valenciennes in Duméril, 1865:374. Holotype, 1,200 mm, Antilles, from Plée.

Diagnosis.—Small sharks, up to 1.37 m long, lacking an interdorsal ridge; snout tip with a dusky to black blotch; tip of second dorsal fin dusky to black as is also leading margin of upper caudal lobe and sometimes trailing margin of lower caudal; snout of moderate length and rounded; internarial width 1.4-1.7 in preoral length; origin of first dorsal fin about over inner pectoral corner; apex of first dorsal sharply rounded; origin of second dorsal over or slightly behind anal fin origin; height of second dorsal 2.6-2.9% TL and 1.1-1.2 in length of its rear tip; dental formula usually $\frac{12-2-12}{11-1-11}$ but may be $\frac{12 \text{ or } 13-1 \text{ or } 2-12 \text{ or } 13}{11 \text{ or } 12-1-11 \text{ or } 12}$ upper teeth moderately narrow, oblique

deeply notched laterally, with uniform serrations; lower teeth slightly oblique, notched laterally, serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 80-88; caudal centra 81-94; total centra 161-180; diplospondyly begins from one-third to halfway along pelvic base; diplospondylous centra either regular in length or with one or two groups of two to four noticeably longer centra in the region between the pelvic and second dorsal fins; penultimate monospondylous centrum 1.0-1.1 wider than long.

Although the western Atlantic *acronotus* shares many similar features with the Indo-west Pacific *dussumieri* and *sealei*, the only species that it might be confused with inside its geographical range is the small and smooth-backed *porosus*. It differs from *porosus* in the position of its second dorsal fin origin (usually slightly behind anal fin origin in *acronotus* but over or slightly behind middle of anal base in *porosus*), in having a dusky to black blotch on the snout tip, usually fewer teeth ($\frac{12-2-12}{11-1-11}$ versus $\frac{14-1-14}{13 \text{ or } 14-0-13 \text{ or } 14}$ in *porosus*), and many more vertebrae.

Nomenclatural discussion.—Although the holotype of *acronotus* is not available there can be no doubt from Poey's (1858-61) description that his species is *acronotus* as recognized by later workers and here. Significant features from Poey's description are: the holotype male was approaching or at maturity ("Les appendices génitaux dépassent considérablement les ventrales, mais sont encore loin de l'anale."), hence near maximum size though only 980 mm long; the presence of six longitudinal ridges on the dermal denticles, which would similarly indicate near maturity; the second dorsal fin was opposite the anal fin; the dental formula was $\frac{13-13}{12-1-12}$ (equivalent to $\frac{12-2-12}{12-1-12}$); the descriptions and illustrations of the teeth, particularly the illustration of a lower tooth, fit *acronotus* very closely; the presence of a pointed nasal lobe; and the origin of the first dorsal fin just behind the pectoral fin.

Poey does not mention the black or dusky spot on the tip of the snout. This may mean that he overlooked it, or alternatively it might not have been obvious due to the age of the specimen or as a result of preservation, for according to Springer (1938:21) "While a black or darker colored nose is a good field recognition mark for fresh specimens, I am not sure that the color would be especially noticeable on preserved ones. The nose spot is well marked on young, but becomes obscure and diffuse on old adults." All specimens I have examined have had dark snout tips, albeit faintly in some cases; however, I was searching for this feature which otherwise might well have been overlooked.

The holotype of *remotus* Valenciennes in Duméril (1865) is a mounted skin of a female about 1,135 mm long from the Antilles. The original description of the type is brief, as was noted by Bigelow and Schroeder (1948:400, footnote) who commented that the correctness of current identifications of *remotus* "...can be tested only by re-examination of the type specimen, now or formerly in the Paris Museum." I have examined the type, taken some measurements, and have been supplied with a more complete set of measurements and a photograph by M. L. Bauchot of the Paris Museum. There is no doubt that Valenciennes' description was based on the type; there is complete agreement between the two except in the phrase that the second dorsal is "plus haute que longue" which is not borne out by measurements. Other features in which there is agreement, including a markedly long space between the dorsal fins (three times the length of the first dorsal base), a long space⁸ between the first dorsal and pelvic fins (slightly more than the first dorsal base), and a relatively short caudal fin (a little more than one-fifth of total length), are unusual and suggest that the specimen skin was stretched the trunk sector when it was mounted; if this is so, then caution is required in using proportions which are based on total length.

In light of the above, comparison of the type of *remotus* Valenciennes with, on the one hand, *remotus* as recognized by Garrick (1913) and Bigelow and Schroeder (1948) whose accounts have been the main basis for recent interpretations of *remotus* and, on the other hand, *acronotus* indicates that despite many features in common the type of *remotus* agrees much more closely with *acronotus* than with *remotus sensu* Bigelow and Schroeder. Evidence for this is presented in Table 29 covering those features which appear to be diagnostic.

Further support for the view that *remotus* Valenciennes is conspecific with *acronotus* is provided by the dental formula of the form which is $\frac{12-1-12}{10-1-10}$. It is possible, of course, that some teeth were lost when the type was mounted, and this appears to be the case with the lower jaw where at least one tooth series is missing on each side, but the full complement of upper teeth seems to be present.

On the basis of the above I have no hesitation in referring *remotus* Valenciennes to *acronotus* Poey, even though this removes from usage the name *remotus* which has become fairly well established in recent years. The next available name for *remotus sensu* Bigelow and Schroeder is *brachyurus* Günther (see p. 174).

⁸This character is noted in the original description as "distinctif rare" and is the source of the name *remotus* which refers to the wide separation of the pelvic fins from the first dorsal; it is probably because of this character (which I believe to be an artifact from the manner in which the skin was mounted) that *remotus* was regarded as distinct from *acronotus*. Duméril (1865:376, footnote), in whose work the original description of *remotus* appears, was aware of Poey's (1860) account of *acronotus* which he lists but stated, without reason, that *acronotus* and four other species described by Poey at the same time were different from the American species including *remotus* treated in his account.

Table 29.—Proportional dimensions showing that the holotype of *Carcharhinus remotus* agrees more closely with specimens of *C. acronotus* than with specimens of *C. remotus* sensu Bigelow and Schroeder. Range is followed by the mean in parentheses.

	Internarial distance as % TL	Anterior margin pectoral as % TL	Anterior margin pelvic as % TL	Anterior margin pectoral Width pectoral	Second dorsal rear tip Second dorsal height
Holotype of <i>remotus</i> (1,135 mm)	4.8	15.5	5.9	1.7	1.0
<i>acronotus</i> (based on 7 specimens, 382 - 1,064 mm)	4.4-5.1 (4.7)	14.6-15.3 (15.0)	5.7-6.1 (5.9)	1.6-1.8 (1.7)	1.1-1.3 (1.3)
<i>remotus</i> sensu Bigelow and Schroeder (1948) (based on 11 specimens, 660 - 1,257 mm, from the Atlantic, Pacific, and Indian Oceans)	5.3-6.1 (5.8)	16.4-18.3 (17.6)	4.7-5.6 (5.2)	1.9-2.1 (2.0)	1.3-1.8 (1.5)

Description (see also Table 30).—Small sharks, not exceeding 1.4 m TL. Midline of back smooth, lacking an interdorsal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles close-packed, overlapping, subcircular in outline, with three longitudinal ridges and three posterior marginal teeth in embryos and half-grown specimens, and five (occasionally seven) ridges and three to five teeth in subadults and adults.

Snout moderately long and rounded in contour. Anterior margin of eye is slightly forward of front of mouth (exceptionally it may be vertically above it). Nostrils oblique, with broadly ovate apertures, the anterior margin of each with a rather long pointed lobe.

Dental formula $\frac{12-2-12}{11-1-11}$ in seven of eight specimens counted; the eighth specimen had only one upper symphyseal tooth; Poey (1860:336) described the holotype as having 12 teeth on each side of the lower jaw, and Springer (1938:22) reported 10 specimens from Florida with formulae ranging from $\frac{12-1-12}{11-1-11}$ to $\frac{13-2-13}{11-1-11}$. Upper teeth rather narrow, oblique except for first to second series at each side of symphysis, their lateral margins deeply notched, their medial margins straight to convex, both margins finely serrated, the serrations of almost uniform size; two (occasionally one) small symphyseal teeth. Lower teeth much narrower than upper, almost erect on each side of symphysis, slightly oblique toward side of mouth, their lateral margins notched, their medial margins concave, both margins very finely and uniformly serrated (except that in mature males the paramedian teeth are virtually smooth, having serrations only basally and at the tips of the cusps); one symphyseal tooth.

First dorsal fin fairly high, rather narrow apically, the apex sharply rounded; origin of first dorsal either above inner corner of pectoral fin or slightly anterior or posterior to it. Second dorsal fin moderately large and high, almost equal to anal fin; length of second dorsal rear tip 1.1-1.3 times its height; origin of second dorsal over or more often slightly behind anal fin origin. Pectoral fin short, broad basally, but narrow and pointed distally; origin of pectoral fin about below the fourth gill opening; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches at least halfway and more often two-thirds along base of first dorsal.

Color after preservation is gray or grayish brown above, white to cream below; apex of second dorsal fin dusky or with a black margin; dorsal margin of upper lobe of caudal fin and sometimes the trailing margin of lower lobe black edged or dusky; trailing edges of first dorsal fin and of pectoral and pelvic fins may be pale or white; snout tip with a dusky to black blotch, not always obvious.

Vertebral counts of six specimens are given in Table 30 and of another four specimens in Table 31.

Centrum diameter usually greater than centrum length except for longest monospondylous centra at posterior of abdomen which are almost or quite as long as wide.

Four specimens (2 from Puerto Rico, 1 each from Brazil and Florida) of the 10 radiographed show no irregularities in centrum length, but the remaining 6 specimens (5 from Florida, 1 from Louisiana) have one or two groups of elongate centra (resembling monospondylous centra) intercalated among the diplospondylous centra; these groups each contain from two to four elongate centra and are variously sited in the region between the pelvic fin and second dorsal fin. Diplospondyly begins above the anterior third or the middle of the pelvic base. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.89-1.0 (mean 0.94) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.29-1.54 (mean 1.43) in 10 specimens.

The smallest free-living specimen I have seen was 495 mm TL, while the largest embryo was 383 mm. Of the few males seen one of 970 mm TL with a clasper length equal to 4.7% TL was approaching maturity, while one of 1,064 mm was mature with a clasper length of 9.1%. Springer (1938:21) reported that *acronotus* are mature at total lengths of about 1,020 mm and may reach about 1,370 mm. He further noted that full-term embryos have been collected at Englewood, Fla., from January to April, with from three to six per female.

Clark and von Schmidt (1965:27) gave data on 54 specimens from the central Gulf coast of Florida; the data accord with Springer's, but they also reported a gravid female taken on 23 May and containing three embryos 370-390 mm TL; they further reported that maturity (at 1,030 mm TL) is probably reached in 2 yr, with yearlings measuring about 800 mm.

Distribution (see also Material examined).—Although *acronotus* is poorly represented in museum collections it has a fairly wide coastal distribution in the western Atlantic and in the islands of the Caribbean. Specimens seen by me or reported in the literature are from

Table 30.—*Carcharhinus acronotus*, proportional dimensions in percentage of total length.

	♀ embryo 382 mm Florida Key West USNM 127121	♀ 634 mm Florida Englewood USNM 104331	♀ 897 mm Gulf of Mexico off Louisiana USNM 197367	♀ 903 mm West Indies St. Croix UZMK P0690	♂ 970 mm Brazil Espirito Santo SU 52851	♀ 1,004 mm Puerto Rico UPR	♂ 1,064 mm Florida Apalachicola USNM 126115
Snout tip to							
outer nostrils	3.3	3.2	3.2	3.0	3.5	3.0	2.9
eye	7.3	6.9	6.9	6.5	7.1	7.0	6.5
mouth	8.1	7.4	7.4	6.5	7.6	7.5	6.9
1st gill opening	18.4	17.3	17.3	16.2	17.6	16.8	17.3
3d gill opening	21.0	19.5	19.6	18.3	19.9	18.9	19.7
5th gill opening	23.1	21.7	21.2	19.3	21.8	20.9	21.6
pectoral origin	22.6	21.3	19.6	19.3	21.1	20.0	21.1
pelvic origin	46.7	48.2	47.4	48.3	48.8	47.1	49.2
1st dorsal origin	32.2	31.2	29.2	29.4	31.3	30.6	31.4
2d dorsal origin	62.0	62.2	61.3	61.0	64.0	62.7	64.2
anal fin origin	59.8	62.0	60.6	61.0	63.6	62.1	64.2
upper caudal origin	71.6	74.1	73.0	72.6	75.0	74.7	75.6
lower caudal origin	70.8	71.8	72.3	72.1	74.8	74.3	75.1
Nostrils							
distance between inner corners	5.1	4.7	4.4	4.7	4.8	4.8	4.6
Mouth							
width	6.3	7.1	6.5	6.3	7.4	6.9	7.2
length	4.5	3.9	3.5	3.9	4.0	3.8	3.9
Labial furrow lengths							
upper	—	0.4	0.4	0.4	0.5	0.5	0.5
lower	—	0.5	0.4	0.4	0.5	0.4	0.5
Gill opening lengths							
1st	2.2	2.5	2.3	2.3	2.3	2.3	2.3
3d	2.4	3.1	3.0	2.7	3.1	3.1	3.3
5th	2.0	2.3	2.5	2.1	2.5	2.4	2.4
Eye							
horizontal diameter	3.0	1.9	1.7	1.9	1.8	1.8	1.6
1st dorsal fin							
length of base	8.6	9.5	10.2	8.8	8.7	9.5	9.1
length posterior margin	3.1	3.3	3.4	3.9	3.2	3.3	3.0
height	7.8	9.3	9.0	9.8	9.3	9.5	—
2d dorsal fin							
length of base	3.7	3.6	4.1	3.9	3.7	4.1	3.8
length posterior margin	3.1	3.6	3.6	3.8	—	3.6	3.7
height	2.6	2.8	2.7	2.9	2.7	2.8	2.9
Anal fin							
length of base	4.8	5.0	4.4	4.2	4.6	4.6	4.3
length posterior margin	3.3	3.1	3.5	3.7	3.6	3.4	3.3
height	3.7	3.5	3.5	3.6	3.3	3.5	3.2
Pectoral fin							
length of base	5.2	5.5	5.8	5.5	6.2	5.4	5.2
length anterior margin	15.1	14.7	15.1	15.2	15.1	14.6	15.3
length distal margin	10.8	11.2	12.2	10.5	12.3	12.6	11.4
greatest width	8.9	9.1	9.2	8.4	9.6	8.8	8.6
Pelvic fin							
length of base	4.4	5.1	5.2	4.9	5.6	4.9	5.4
length anterior margin	5.8	5.8	6.1	5.7	5.9	6.0	5.8
length distal margin	5.1	4.7	4.7	4.8	5.3	4.9	4.9
length of claspers	—	—	—	—	4.7	—	9.1
Caudal fin							
length of upper lobe	28.3	26.7	27.4	27.3	25.7	26.4	25.2
length of lower lobe	11.6	11.0	11.2	12.3	12.2	11.6	11.7
Trunk at pectoral origin							
width	11.2	11.2	11.1	10.0	10.9	11.0	11.2
height	9.7	11.4	11.1	10.5	11.7	11.7	10.8
Dental formula		12-2-12 11-1-11	12-2-12 11-1-11	12-2-12 11-1-11	12-2-12 11-1-11	12-2-12 11-1-11	12-2-12 11-1-11
Vertebrae							
precaudal	81	84	81		87	88	82
caudal	84	91	86		88	93	85
total	165	175	167		175	181	167

Table 31.—Vertebral numbers in four specimens of *Carcharhinus acronotus*.

Specimens		Precaudal	Caudal	Total
USNM 127120	Florida, Key West	80	87	167
USNM 127122	Florida, Key West	81	83	164
USNM 127123	Florida, Key West	80	81	161
USNM 179038	Puerto Rico	86	94	180
Range (including counts from Table 30)		80-88	81-94	161-181

North Carolina southwards and around the Florida coast to as far west as Louisiana in the Gulf of Mexico; the type of *acronotus* was from Cuba, and the type of *remotus* from the Antilles; J. Randall has provided material from Puerto Rico and Erdman (1956:321) has also reported it from Puerto Rico; I have seen one specimen from the Virgin Islands (St. Croix); Cervigon (1966:38) gave an account of several specimens from Venezuela (from Cubagua and La Blanquilla) and Lowe (McConnell) (1962:680) reported *acronotus* from British Guiana; and there are a few specimens from Brazil (from off Vitória and Rio de Janeiro). The species is undoubtedly present throughout more of the West Indies and along more of the east coast of South America than present records would indicate.

Material examined.—USNM 127120, female embryo, 362 mm, Florida, Key West, I. Ginsburg; USNM 127123, male embryo, 375 mm, Florida, Key West, I. Ginsburg; USNM 127121, female embryo, 382 mm, Florida, Key West, I. Ginsburg; USNM 127122, male embryo, 383 mm, Florida, Key West, I. Ginsburg; ZSZM 8190, female, 495 mm, North Carolina, Carteret County, 23 December 1899, H. H. and C. S. Brinsley; USNM 104331, female, 634 mm, Florida, off Englewood, 1937, S. Springer; USNM 30679, female, 775 mm, skin, Florida, Pensacola, 1882, S. Stearns; USNM 179038, female, about 830 mm, Puerto Rico, La Pasguera, 30 April 1963, J. E. Randall; USNM 197367, female, 897 mm, Gulf of Mexico, off Louisiana, 28°25'N, 92°12'W, 15 November 1961, Oregon; UZMK PO690, female, 903 mm, West Indies, St. Croix, 18 September 1845; SU 52851, male, 970 mm, Brazil, Espirito Santo, Vitória, 17 August 1944; UPR (no number), female, 1,004 mm, Puerto Rico, Tres Hermanos, 28 January 1963, J. Randall; USNM 126115, mature male, 1,064 mm, Florida, Apalachicola, West Pass, 24 June 1932; USNM 127126, skin of mature male, about 1,070 mm, Florida, Apalachicola, West Pass, 24 June 1932; MNHN A 9661, mounted skin of female, 1,135 mm [holotype of *Carcharias (Prionodon) remotus*], Antilles, Plée.

Carcharhinus porosus (Ranzani, 1840)

Figures 36, 37

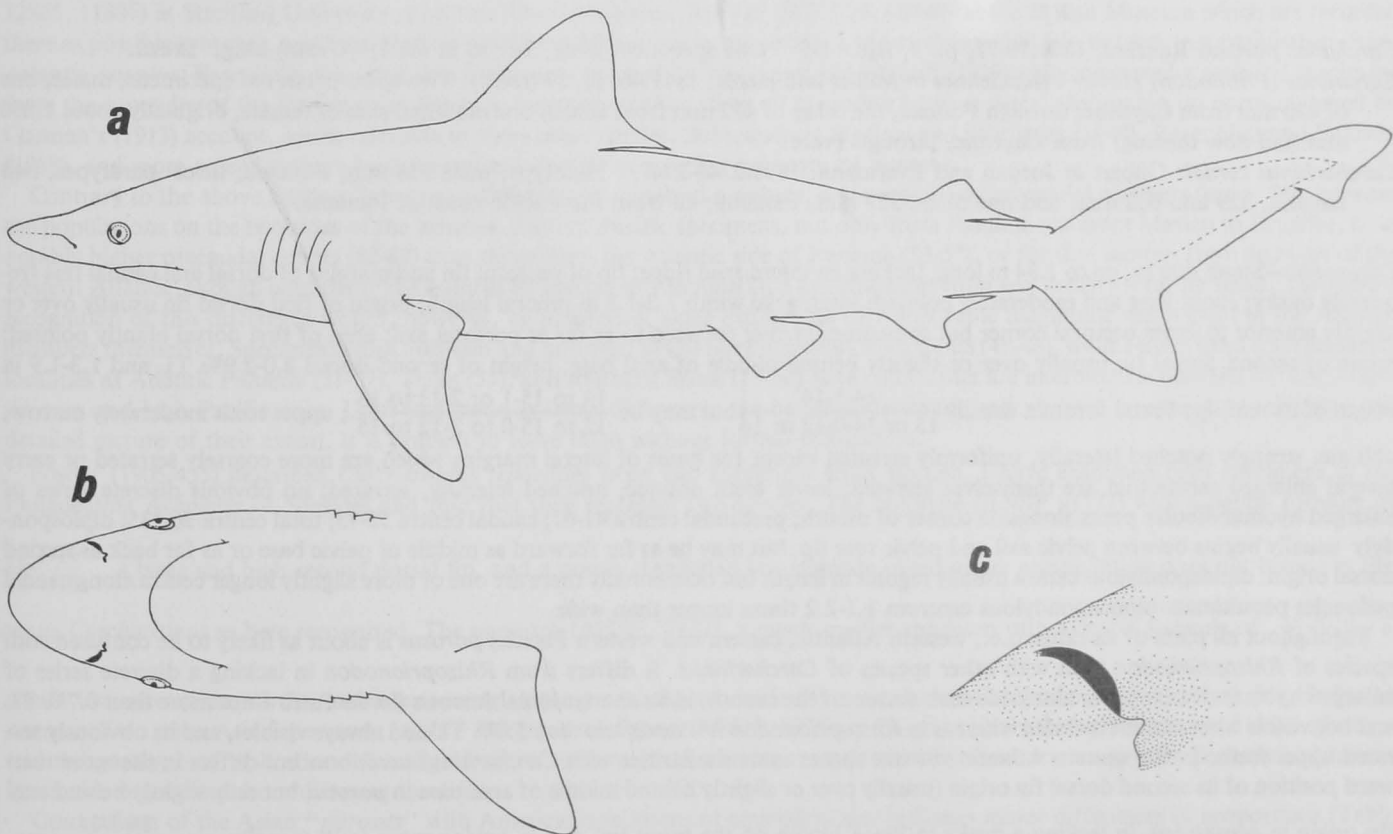


Figure 36.—*Carcharhinus porosus*: a, left side of UCLA 58-128, 860 mm TL, female from Pacific Panama; b, enlarged left nostril of same; c, underside of head of USNM 181339, 541 mm TL, female from Pacific Mexico.

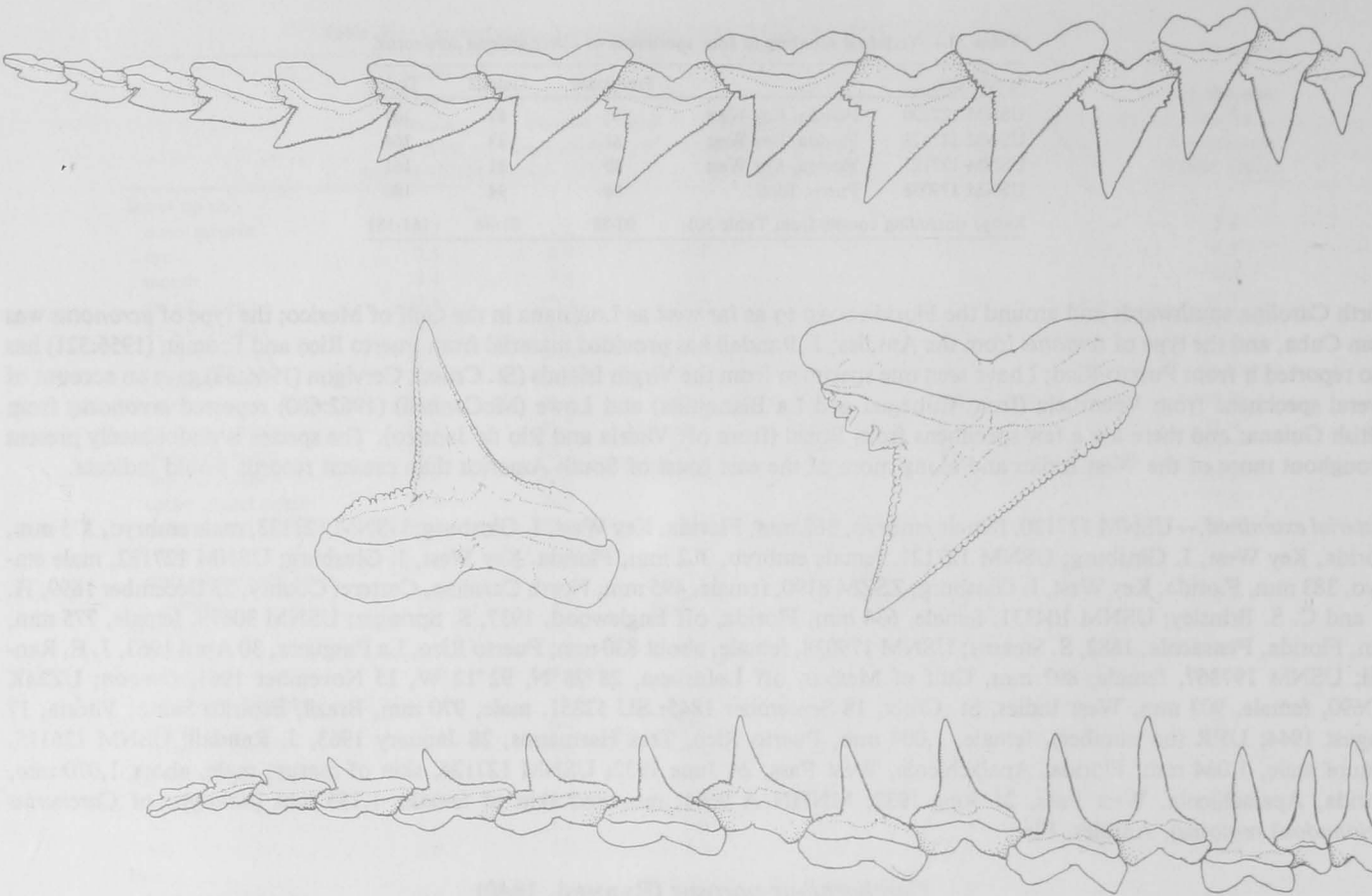


Figure 37.—*Carcharhinus porosus*, USNM 181336, 554 mm TL, female from Pacific Mexico: right upper and lower teeth (symphysis to the right); inset teeth are enlarged sixth upper tooth and fifth lower teeth.

Carcharias porosus Ranzani, 1840:70-71, pl. 9, figs. 1-5. One specimen, male, 3 ft 10 in (ca 1,170 mm) long, Brazil.

Carcharias (Prionodon) Henlei Valenciennes in Müller and Henle, 1841:46, pl. 19 (teeth). Two spirit-preserved specimens, males, one of 420 mm from Cayenne, through Poiteau, the other of 422 mm from Brazil; one mounted skin of female, originally about 1,200 mm (tail now missing) from Cayenne, through Frère.

Carcharhinus cerdale Gilbert in Jordan and Evermann, 1898:2746-2747. Holotype, male 558 mm, Panama; three paratypes, two females, 329 and 602 mm, and one male, 527 mm, Panama; all from the Pacific coast of Panama.

Diagnosis.—Small sharks, up to 1.34 m long, lacking an interdorsal ridge; tip of pectoral fin and margins of dorsal and caudal fins frequently dusky; snout long and moderately pointed; internarial width 1.2-1.8 in preoral length; origin of first dorsal fin usually over or slightly anterior to inner pectoral corner but sometimes farther forward to as far as pectoral axil; apex of first dorsal bluntly pointed; origin of second dorsal fin usually over or slightly behind middle of anal base; height of second dorsal 2.0-2.9% TL and 1.3-1.9 in length of its rear tip; dental formula usually $\frac{14-1-14}{13 \text{ or } 14-0-13 \text{ or } 14}$ but may be $\frac{13 \text{ to } 15-1 \text{ or } 2-13 \text{ to } 15}{12 \text{ to } 15-0 \text{ or } 2-12 \text{ to } 15}$; upper teeth moderately narrow, oblique, strongly notched laterally, uniformly serrated except for bases of lateral margins which are more coarsely serrated or carry several enlarged serrae that are themselves serrated; lower teeth oblique, notched laterally, serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 41-67; caudal centra 55-73; total centra 96-135; diplospondyly usually begins between pelvic axil and pelvic rear tip, but may be as far forward as middle of pelvic base or as far back as second dorsal origin; diplospondylous centra usually regular in length but occasionally there are one or more slightly longer centra along caudal peduncle; penultimate monospondylous centrum 1.1-2.2 times longer than wide.

Throughout all parts of its range (i.e., western Atlantic, eastern and western Pacific) *porosus* is about as likely to be confused with species of *Rhizoprionodon* than with other species of *Carcharhinus*. It differs from *Rhizoprionodon* in lacking a discrete series of enlarged hyomandibular pores alongside each corner of the mouth, in its shorter labial furrows (lower furrow not more than 0.7% TL and not visible when mouth is closed whereas in *Rhizoprionodon* it is never less than 1.0% TL and always visible), and its obviously serrated upper teeth. In the western Atlantic *porosus* shares some similarities with *Carcharhinus acronotus* but differs in the more rearward position of its second dorsal fin origin (usually over or slightly behind middle of anal base in *porosus* but only slightly behind anal fin origin in *acronotus*), in lacking a dusky to black blotch on the snout tip, and in having more teeth (usually $\frac{14-1-14}{13 \text{ or } 14-0-13 \text{ or } 14}$ compared with $\frac{12-2-12}{11-1-11}$). In the western Pacific *porosus* and *borneensis* are markedly alike, but *borneensis* has a discrete series of

enlarged hyomandibular pores (such as in *Rhizoprionodon*), a much lower second dorsal fin (its height 2.2-2.4 in length of its rear tip versus 1.3-1.9 in *porosus*) and fewer teeth (usually $\frac{12-1-12}{11-1-11}$).

Nomenclatural discussion.—Although I have no information on the fate of the male specimen, about 1,170 mm, from Brazil, on which Ranzani (1840:70, pl. 9) based his account of *porosus*, his description of it is good and this, coupled with his excellent illustrations, eliminates the possibility of confusion with any other species, including even the superficially very similar *Rhizoprionodon lalandei* and *R. porosus*, known to occur in the same region.

Duméril (1865:372) observed that the three syntypes of *henlei* Valenciennes in Müller and Henle, 1841 in the Paris Museum included two species. One of these syntypes, which he assigned to *henlei*, was “un individu unique, de l^m.23, pris à Cayenne par M. Frère.” The other two syntypes, small, spirit-preserved specimens, “longs de 0^m.42 et de 0^m.45, proviennent, le premier du Brésil, et le second de Cayenne, par les soins de Pointeau,” he assigned to *porosus* Ranzani, with the comment that “Ils sont mentionnés par MM. Müller et Henle dans la description du *C. (Pr.) Henlei*; mais la comparaison avec le type véritable de cette dernière espèce ne permet pas la confusion.” He noted further that Müller and Henle did not appear to have known about Ranzani’s species. I have examined the above three syntypes, which are still in the Paris Museum even though Bertin (1939) listed only the largest in his catalogue of types, and I can confirm Duméril’s findings that they represent two species. The largest specimen (MNHN A9657) is a mounted skin, in very poor condition with the tail and anal fin missing, measuring 920 mm excluding the tail; it appears to be a specimen of *obscurus* Lesueur, 1818. The two smaller specimens (MNHN 1139 and 1140), males of 420 and 422 mm, respectively, are in good condition, and both are clearly referable to *porosus*.

Duméril’s statements about the largest syntype, including particularly the words “un individu unique” and “le type véritable” could be interpreted as designating it as lectotype of *henlei*. The effect of this would be to make *henlei* a junior synonym of *obscurus*—a result which is not only at variance with subsequent interpretations of *henlei* but which also appears not to be in accord with the description of *henlei* by Valenciennes in Müller and Henle (1841:46). The original description of *henlei* is rather brief and general, and the only illustrations are of an upper and lower tooth which are so poorly drawn as not to be clearly representative of either *obscurus* or *porosus*. However, the description states that the second dorsal fin is over the posterior end of the anal fin (thus indicating *porosus*), and the only specimen for which Valenciennes gave measurements had a total length of 17 in 3 lines or 454 mm (close to the lengths of the smaller syntypes which are *porosus*). In view of the above I choose not to accept Duméril’s statements as being a clear indication of lectotype designation and instead designate MNHN 1140, a male of 422 mm from Cayenne, as lectotype of *henlei*, thus ensuring that current interpretations of *henlei* as a junior synonym of *porosus* are maintained.

The description of *cerdale* Gilbert in Jordan and Evermann (1898:2746) from Pacific Panama is excellent and, although it is not accompanied by illustrations, its agreement with *porosus* is obvious. Gilbert did not compare it with the Atlantic *porosus* but only with Pacific *aethalorus* (= *limbatus*). I have examined the holotype (SU 11884), which was the only type material mentioned by Gilbert though he noted that *cerdale* was abundant at Panama and that numerous specimens were obtained, and three paratypes (SU 12866, 12865, 11886) at Stanford University, plus two other specimens (BMNH 1903.5.15.339-40) at the British Museum which are recorded there as possible syntypes, and I can find no consistent differences in proportions, external morphology, or teeth to separate them from Atlantic *porosus*. Essentially the same conclusion was reached by Meek and Hildebrand (1923) who compared a series of specimens from the two sides of the Panamanian isthmus, but they ascribed them all to *cerdale* because their information on *porosus*, based on Garman’s (1913) account, seems referable to some other species. Subsequently Bigelow and Schroeder (1948), Rosenblatt and Baldwin (1958), and more recent authors have recognized *cerdale* as a junior synonym of *porosus*.

Contrary to the above findings is a strong difference in vertebral numbers, and particularly precaudal numbers (see p. 76), between the populations on the two sides of the isthmus. Eastern Pacific specimens, not only from Panama but from Mexico to Ecuador, have notably higher precaudal counts (62-67) than those from the Atlantic side of Panama (53-57), or for that matter, from any part of the western Atlantic, though admittedly the number of specimens examined for this character from any locality is rather small. Taxonomic recognition of this difference would, however, be ill-advised, since differences of comparable magnitude are evident in the Atlantic members themselves. Specimens from Surinam and northern Brazil have markedly low counts (41-48), while others from such disparate localities as Atlantic Panama (53-57), Texas (55), and southern Brazil (53-56) have counts that are intermediate between the low Atlantic ones and high Pacific ones. Until such time as these differences are better understood, and we have a more comprehensive and detailed picture of their extent, it is prudent to leave them without formal recognition.

Fowler (1905:455) described *Carcharhinus tephrodes* from two specimens from Borneo. I have examined both specimens in the Philadelphia Academy of Sciences and find that they represent two species. The holotype (ANSP 91177) with a dental formula of

$\frac{19-1-19}{18-1-18}$, a large and high second dorsal fin, and a poorly developed but elongate ovoid upper precaudal pit does not belong in the genus *Carcharhinus* as here recognized. The paratype (ANSP 77121), a much smaller specimen with a dental formula of $\frac{13-2-13}{14-1-14}$, a

small, low second dorsal fin, and a transverse upper precaudal pit, is clearly a species of *Carcharhinus* and remarkably similar to *porosus*. Two other Asian specimens (ANSP 76859 from Saigon; NMV 61-463 from Bangkok) have the same facies, and although these and the paratype of *tephrodes* differ slightly from each other in some features, the differences are not greater than those between specimens of *porosus* from different localities.

Comparison of the Asian “*porosus*” with American specimens of equivalent size indicates minor differences in proportions (Table 32). In particular the Asian specimens are, on average, relatively longer tailed and broader headed and have longer pectorals and higher first dorsal fins. Because of their longer tails, their proportions measured from snout tip to various regions of the snout, head, and body are smaller relative to total length. In addition, the first dorsal fin origin is slightly farther forward relative to the pectoral base

Table 32.—Proportional dimensions showing differences between Asian and American specimens of *Carcharhinus porosus*. Measurements are ranges and (means) given as percentages of total length.

	Asian specimens (3♀, 340-433 mm)	American specimens (3♀, 351-460 mm; 3♂, 312-388 mm)
Snout tip to		
outer nostrils	3.7- 4.6 (4.3)	4.3- 5.3 (4.8)
eye	7.1- 8.5 (7.9)	7.9- 9.3 (8.6)
mouth	7.4- 9.2 (8.5)	8.3- 9.6 (9.0)
5th gill opening	22.5-25.8 (24.2)	22.8-25.8 (24.6)
1st dorsal origin	27.9-31.8 (29.5)	31.5-33.4 (32.3)
2d dorsal origin	60.9-63.3 (62.3)	61.5-66.2 (64.3)
upper caudal origin	71.0-75.0 (72.9)	74.0-78.1 (76.2)
Caudal		
length upper lobe	25.2-28.8 (27.3)	23.0-26.2 (24.2)
Mouth width	7.8- 8.5 (8.2)	7.0- 7.8 (7.4)
Head width	13.1-13.4 (13.3)	11.6-12.6 (12.3)
Internarial distance	6.0- 6.6 (6.3)	5.4- 6.0 (5.7)
Pectoral		
length anterior margin	14.4-16.7 (15.5)	13.2-15.1 (14.1)
1st dorsal, height	7.6- 9.8 (8.5)	6.9- 8.9 (8.0)
2d dorsal, height	2.0- 2.3 (2.2)	2.2- 2.5 (2.3)

(from above the pectoral axil to halfway along the pectoral inner margin in the Asian specimens, but from halfway along the pectoral inner margin to above the pectoral inner corner in the American specimens).

In considering the value which should be placed on the above minor differences for determining the status of the Asian specimens, it must be borne in mind that with only one exception (head width 13.1-13.4% versus 11.6-12.6%) there is overlap with the American specimens. Furthermore, most if not all of the proportions listed vary with growth, and hence the ranges given in Table 32 will not generally apply if specimens of larger size were considered. No adults of the Asian form were found for study, and hence no firm criteria, other than geographic locality, can be put forward to distinguish the Asian from the American forms. In view of this, and the fact that vertebral counts of the Asian specimens lie within the middle of the total range of counts for the American specimens, I favor recognizing the Asian and American forms as conspecific, despite the seemingly improbable distribution for a small, essentially tropical, littoral shark which results from that decision.

Suggestions that *porosus* may occur in the eastern Atlantic (North Africa) have been based on Bennett's (1831:148) account of *Carcharias fissidens* which was tentatively placed in the synonymy of *porosus* by Dumeril (1865), Günther (1870), and Bigelow and Schroeder (1948). I can find no support for this referral. Bennett's very brief and inadequate description mentions the second dorsal fin beginning above the middle of the anal fin, and the teeth each with a single, very oblique cusp, but these features could as well apply to species of *Rhizoprionodon* as to *porosus*. Moreover, Bennett states that the teeth were as figured in Lacépède (1798, vol. 1, pl. 8, fig. 2) and the teeth shown in that illustration are clearly smooth edged, thereby increasing the likelihood that Bennett described a species of *Rhizoprionodon*. Further supporting evidence is that no other material of *porosus* has been reported from the eastern Atlantic despite extensive collecting in that region, but *Rhizoprionodon* is represented there by *R. acutus* (see Springer 1964). Bennett did not list type material but if types of *fissidens* were to be found and prove to be conspecific with *acutus*, it should be noted that Bennett's description (1831) precedes that of *acutus* Rüppell 1837. Fourmanoir's (1961) report of one specimen from Madagascar as *Carcharinus porosus* Ranzani lacks sufficient data to give an unequivocal identification, but his illustrations of two teeth suggest that he, also, was dealing with *R. acutus*.

Description (see also Tables 33, 34).—Small sharks, not exceeding 1.5 m TL. Midline of back between dorsal fins smooth, lacking an interdorsal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles spaced so that in general they are scarcely or not overlapping, subcircular in small specimens but noticeably wider than long in large specimens, each with three longitudinal ridges and corresponding posterior marginal teeth, the latter greatly reduced in denticles from adults.

Snout long and moderately pointed in contour. Anterior margin of eye is over or slightly forward of front of mouth. Nostrils strongly oblique, slitlike, the anterior margin of each with a prominent, pointed lobe.

Dental formula $\frac{14 \text{ or } 15-1 \text{ or } 2-14 \text{ or } 15}{14 \text{ or } 15-0 \text{ to } 2-14 \text{ or } 15}$ in 7 of 15 specimens counted; $\frac{13 \text{ or } 14-1 \text{ or } 2-13 \text{ or } 14}{13 \text{ or } 14-0 \text{ to } 2-12 \text{ to } 14}$ in 4; $\frac{13-1-13}{13-13}$ in 3; and $\frac{15-1-15}{13-2-13}$ in 1.

Upper teeth moderately narrow, oblique except for the first one or two series on each side of symphysis, their lateral margins strongly notched, their medial margins straight or slightly concave, both margins serrated; basally the lateral margins are more coarsely serrated or carry several enlarged serrae which themselves are serrated; one or infrequently two symphysial teeth. Lower teeth narrow, erect or almost so at center of mouth but becoming increasingly oblique towards the sides where the teeth are definitely notched on their lateral margins; both margins finely serrated, the serrations coarser or more irregular basally on the lateral margins; usually either two symphysial teeth or else there are none at the symphysis itself but the two central teeth are smaller than those laterally adjacent; occasionally there is one small symphysial tooth.

First dorsal fin low, erect, nearly symmetrical, its apex bluntly pointed; origin of first dorsal in American specimens usually somewhat anterior to or over inner (posterior) corner of pectoral fin, but in some specimens it is farther forward, not infrequently

Table 33.—*Carcharhinus porosus* (American specimens), proportional dimensions in percentage of total length.

	♂ 312 mm Brazil Maranhão SU 52746	♂ 317 mm Panama Chame Point USNM 82707	♀ 351 mm Texas Galveston USNM 196798	♂ 388 mm Ecuador USNM 53511	♀ 460 mm Panama Colon CNHM 8157	♀ 541 mm Mexico San Blas USNM 181339	1♂ 558 mm Panama SU 11884	♀ 572 mm Mexico San Blas USNM 181336	♂ 745 mm Panama MCZ 709	♀ 885 mm Panama MCZ 70
Snout tip to										
outer nostrils	5.3	5.0	4.3	4.6	4.6	5.4	4.7	5.2	4.3	4.4
eye	9.3	9.1	8.3	8.5	7.9	9.2	8.6	8.9	8.0	7.7
mouth	9.6	9.5	8.8	8.8	8.3	9.6	8.6	9.1	7.8	7.9
1st gill opening	20.6	20.8	19.1	20.1	18.7	22.5	20.2	18.9	19.2	18.4
3d gill opening	22.6	23.0	21.9	—	21.1	25.0	—	21.7	21.7	—
5th gill opening	24.7	25.2	24.2	25.8	22.8	26.8	25.1	25.0	23.6	23.6
pectoral origin	24.1	24.6	23.7	25.0	21.9	26.1	24.3	23.8	22.5	22.5
pelvic origin	48.4	48.7	47.8	48.2	48.2	50.3	48.7	50.2	48.2	49.1
1st dorsal origin	31.6	33.4	31.9	32.7	31.5	33.4	34.0	32.0	32.5	32.8
2d dorsal origin	64.4	65.6	61.5	64.2	63.7	66.5	65.7	64.7	65.2	66.7
anal fin origin	61.5	62.8	60.4	61.9	61.1	64.2	63.3	62.9	62.4	63.3
upper caudal origin	75.6	77.5	74.0	76.3	75.4	77.8	76.9	75.7	76.3	76.3
lower caudal origin	73.7	76.0	72.4	75.0	73.5	76.3	75.3	74.1	75.0	74.2
Nostrils										
distance between										
inner corners	5.6	6.0	6.0	5.4	5.4	5.4	5.4	5.4	5.0	5.2
Mouth										
width	7.5	7.2	7.8	7.0	7.4	8.3	7.7	8.2	7.8	7.9
length	4.9	5.0	4.7	5.2	4.6	5.0	5.2	4.5	5.2	5.1
Labial furrow lengths										
upper	0.5	0.5	0.4	0.3	0.5	0.5	0.4	0.3	0.5	0.6
lower	0.4	0.6	0.5	0.5	0.5	0.6	0.5	0.7	0.6	0.5
Gill opening lengths										
1st	2.4	2.4	2.6	2.8	2.6	2.3	2.9	2.4	2.7	2.9
3d	2.8	2.8	3.3	3.1	2.8	2.9	3.0	3.3	3.2	3.4
5th	2.3	1.9	2.3	2.2	2.3	2.4	2.2	—	2.4	2.8
Eye										
horizontal diameter	2.5	2.4	2.4	2.3	2.2	2.1	2.0	2.1	1.8	1.6
1st dorsal fin										
length of base	10.4	10.1	9.1	10.3	9.9	10.5	9.7	11.2	10.1	10.6
length posterior margin	4.6	4.4	4.6	4.4	4.7	5.4	4.5	5.1	4.4	5.0
height	7.0	6.9	8.8	8.2	8.9	9.2	8.4	9.4	8.9	9.9
2d dorsal fin										
length of base	3.4	3.6	4.0	4.1	3.4	4.2	4.1	4.5	3.1	3.2
length posterior margin	3.5	3.6	4.0	3.6	4.1	3.7	3.8	3.8	3.5	3.6
height	2.2	2.4	2.5	2.3	2.2	2.6	2.5	2.8	2.3	2.7
Anal fin										
length of base	4.3	4.4	4.3	4.4	4.6	5.0	4.4	4.7	4.3	3.8
length posterior margin	3.5	3.5	3.6	3.6	3.9	3.7	3.6	4.0	3.4	4.0
height	2.9	3.0	3.4	3.1	2.9	2.9	3.3	3.3	3.2	3.2
Pectoral fin										
length of base	5.5	5.7	6.0	5.2	5.4	6.1	6.1	6.1	5.9	5.9
length anterior margin	13.6	13.2	13.9	14.9	13.9	15.9	15.0	16.4	15.8	16.4
length distal margin	8.0	9.0	10.5	10.3	11.5	12.4	11.5	13.6	12.2	14.0
greatest width	8.0	8.8	9.0	8.2	9.1	10.5	9.3	9.8	—	9.8
Pelvic fin										
length of base	3.8	4.7	4.4	4.6	4.6	5.0	4.3	4.7	4.2	5.0
length anterior margin	5.1	5.2	5.3	5.7	5.4	5.2	4.9	5.2	4.8	5.8
length distal margin	4.0	5.2	4.8	4.4	4.6	5.2	5.0	5.8	5.2	5.5
length of claspers	1.9	1.9	—	1.8	—	—	2.2	—	2.7	—
Caudal fin										
length dorsal lobe	24.3	23.0	26.2	23.2	24.5	24.2	24.5	25.0	23.9	23.8
length ventral lobe	11.2	9.1	10.5	10.5	11.5	11.1	10.9	11.2	11.4	11.1
Trunk at pectoral origin										
width	11.2	11.3	12.0	11.1	11.9	12.6	11.6	12.4	12.7	12.6
height	10.4	11.8	11.7	9.8	10.2	11.6	11.3	11.5	—	11.4
Dental formula	$\frac{13-1-13}{13-13}$	—	$\frac{13-1-13}{13-13}$	$\frac{14-1-14}{14-1-14}$	$\frac{14-1-14}{13-13}$	$\frac{15-1-15}{13-2-13}$	—	$\frac{15-1-14}{14-14}$	$\frac{14-1-15}{13-2-14}$	$\frac{14-1-14}{14-2-14}$
Vertebrae										
precaudal	41	64	55	67	55	62	64	62	—	—
caudal	55	64	66	67	61	70	65	73	—	—
total	96	128	121	134	116	132	129	135	—	—

¹Holotype of *Carcharhinus cerdale* Gilbert.

Table 34.—*Carcharhinus porosus* (Asian specimens), proportional dimensions in percentage of total length.

	♀ 340 mm Saigon ANSP 76859	♂ 365 mm Borneo ANSP 77121	♀ 433 mm Bangkok NMV 61-463
Snout tip to			
outer nostrils	3.7	4.5	4.6
eye	7.1	8.2	8.5
mouth	7.4	9.0	9.2
1st gill opening	18.8	21.3	20.1
3d gill opening	21.0	24.1	22.0
5th gill opening	22.5	25.8	24.2
pectoral origin	21.5	24.4	23.8
pelvic origin	46.4	49.0	48.0
1st dorsal origin	27.9	28.8	31.8
2d dorsal origin	60.9	62.6	63.3
anal fin origin	58.4	60.8	60.7
upper caudal origin	71.0	72.6	75.0
lower caudal origin	69.4	71.8	73.6
Nostrils			
distance between inner corners	6.2	6.6	6.0
Mouth			
width	8.5	8.2	7.8
length	4.3	5.1	4.6
Labial furrow lengths			
upper	0.6	0.4	0.3
lower	0.4	0.4	0.6
Gill opening lengths			
1st	2.1	2.2	2.7
3d	2.5	2.5	3.3
5th	2.2	2.2	2.4
Eye			
horizontal diameter	2.4	2.2	2.4
1st dorsal fin			
length of base	11.5	11.8	9.5
length posterior margin	4.6	6.0	—
height	7.6	9.8	8.1
2d dorsal fin			
length of base	3.2	4.1	3.6
length posterior margin	3.5	4.1	3.5
height	2.3	2.2	2.0
Anal fin			
length of base	4.5	4.7	4.6
length posterior margin	3.4	3.8	3.3
height	2.8	2.7	2.8
Pectoral fin			
length of base	5.9	6.6	5.8
length anterior margin	15.3	16.7	14.4
length distal margin	9.7	12.9	10.8
greatest width	8.5	9.3	8.9
Pelvic fin			
length of base	4.7	4.5	4.5
length anterior margin	5.1	5.3	4.8
length distal margin	5.0	5.2	4.4
length of claspers	—	—	—
Caudal			
length dorsal lobe	28.8	28.0	25.2
length ventral lobe	11.5	11.5	10.5
Trunk at pectoral origin			
width	12.6	11.8	12.0
height	12.1	10.4	10.4
Dental formula	$\frac{1-14-1-14-1}{14-1-14}$	$\frac{14-1-14}{14-1-14}$	$\frac{13-1-13}{13-1-13}$
Vertebrae			
precaudal	57	57	54
caudal	59	61	66
total	116	118	120

¹Paratype of *Carcharhinus tephrodes* Fowler.

about halfway along the inner pectoral margin and exceptionally nearer to the axil than to the corner; in one of the three Asian specimens it is over the axil, and in the other two it is one-third and halfway along the inner pectoral margin, respectively. Second dorsal fin moderately low, slightly smaller than anal fin; length of second dorsal rear tip 1.3-1.9 (mean 1.5) times second dorsal height in 15 American specimens, and 1.6-1.9 (mean 1.8) times in the 3 Asian specimens; origin of second dorsal usually over or slightly behind middle of anal base, but fairly variable (ranging from one-fourth to four-fifths along anal base in 14 American specimens and from one-third to almost three-fifths along anal base in the 3 Asian specimens). Pectoral fins short, with only moderately pointed outer tips; origin of pectorals usually below the level of the fourth gill openings or below and between the levels of the fourth and fifth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches from just behind level of middle of dorsal base to as far as first dorsal axil.

Color (presumably in life) was described by Gilbert *in* Jordan and Evermann (1898) as "Color varying from light to dark gray above, the belly and lower part of sides whitish; fins all dusky or grayish, the caudal often with a blackish border; pectoral with or without a black tip, the latter . . . usually not extended into inner face of fin." After preservation in alcohol, there is little change except that the overall color is brownish gray; some specimens (perhaps all in life) have a short horizontal pale band along the midlevel of the side; the tip of the underside of the pectoral fin is frequently slightly dusky, and sometimes there are narrow dusky margins on the caudal fin and first and second dorsal fins.

Vertebral counts of 11 specimens are given in Tables 33 and 34 and of another 35 specimens in Table 35.

As shown in Table 36 (which excludes three specimens for which the locality data are questionable), the lowest precaudal counts occur in specimens from Surinam and north Brazil and the highest in specimens from the eastern Pacific. Intermediate counts occur in specimens from such wide-spaced localities as south Brazil, Atlantic Panama, and Texas, and Asia (Borneo, Thailand, Vietnam). Caudal counts show a similar but less marked distribution.

Centrum diameter greater than centrum length except in the last third or more of the monospondylous centra whose lengths range from slightly more than their diameters to more than twice their diameters (the latter in one specimen each from north Brazil and Surinam). Diplospondylous centrum length usually regular, though a few specimens with irregularities in the form of one or more slightly longer centra interposed between the normal centra along the caudal peduncle. Diplospondyly at various distances behind the pelvic fin base, the only exception in 33 specimens being the one from Texas where it is above the middle of the pelvic base. The commonest site of diplospondyly is between the pelvic axil and pelvic rear tip, but in many specimens it is farther rearward, to as far as the anal fin origin, and in one specimen each from north Brazil and Surinam it is almost or quite at the level of the second dorsal fin origin.

Table 35.—Vertebral numbers in 35 specimens of *Carcharhinus porosus*.

Specimens		Precaudal	Caudal	Total
	Surinam ¹	44	57	101
	Surinam ¹	46	57	103
USNM 156722	Surinam	47	61	108
	Surinam ²	48	60	108
USNM 79317	Panama, Colon	53	59	112
UZMK PO 685	Brazil, Cotinguiba (= ?)	53	65	118
	10 specimens, Brazil, Cananéia ²	53-56 (mean 54.2)	59-65 (mean 62.4)	112-120 (mean 116.7)
USNM 79300	Panama (Atlantic?) ³	53	63	116
SU 52760	Brazil, Vitória	54	64	118
USNM 79316	Panama, Colon	55	64	119
USNM 79323	Panama, Colon	56	63	119
USNM 79298	Panama, (Atlantic?) ³	57	60	117
USNM 79286	Panama, Colon	57	65	122
SU 9293	Ecuador, Guayaquil	62	67	129
SU 9293	Ecuador, Guayaquil	62	67	129
SU 12865	Panama, Pacific ⁴	63	65	128
SU 12866	Panama, Pacific ⁴	63	67	130
USNM 82707	Panama, Chame Point	64	63	127
SU 11886	Panama, Pacific ⁴	64	65	129
USNM 88676	Ecuador, Guayaquil	64	66	130
USNM 88676	Ecuador, Guayaquil	64	67	131
USNM 82707	Panama, Chame Point	64	69	133
USNM 82707	Panama, Chame Point	65	64	129
USNM 82707	Panama, Chame Point	65	65	130
USNM 181336	Mexico, San Blas	67	68	135
Range (including counts from Tables 33, 34)		41-67	55-73	96-135

¹Counts from radiographs supplied by S. Springer, Bureau of Commercial Fisheries, Stanford University, Stanford, CA 94305, pers. commun. October 1965.

²Counts supplied by V. Sadowsky, Chief Oceanographer, Instituto Oceanografico, Universidade de São Paulo, Cananéia, Brazil, pers. commun. December 1965.

³Supposedly from Panama City Fish Market, but the low precaudal count suggests it was from the Atlantic rather than the Pacific. One of these specimens (USNM 79300) was collected on the same day as others (USNM 79286, 79302) recorded from Colon, thus suggesting there was an error in transcribing the locality data.

⁴Paratypes of *Carcharhinus cerdale*.

Table 36.—Frequency distribution of precaudal and caudal vertebral numbers in *Carcharhinus porosus* (arrowed ranges with a number in the middle are data from other authors).

Locality	Precaudal																	Caudal																																
	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73				
Surinam and North Brazil	1			1		1	1	1																				1	2			1	1																	
South Brazil														1																																				
														← 10 →																																				
Atlantic Panama and Texas													1		3	2	1																																	
Borneo, Thailand, Vietnam													1				2																																	
Eastern Pacific (Mexico to Ecuador)																																																		

Table 37.—Proportional dimensions of penultimate monospondylous centrum and first diplospondylous centrum in 31 specimens of *Carcharhinus porosus*.

Ratio		Locality	Range	Mean	n
$\frac{\text{Length}}{\text{Diameter}}$ of penultimate monospondylous centrum		Surinam and North Brazil	1.71-2.20	1.96	5
		South Brazil	1.80		1
		Atlantic Panama and Texas	1.36-1.63	1.46	5
		Borneo, Thailand, Vietnam	1.23-1.86	1.44	3
		Eastern Pacific	1.10-1.54	1.29	17
		All localities	1.10-2.20	1.46	31
$\frac{\text{Length penultimate monospondylous centrum}}{\text{Length first diplospondylous centrum}}$		Surinam and North Brazil	1.73-2.04	1.90	5
		South Brazil	1.71		1
		Borneo, Thailand, Vietnam	1.54-1.86	1.71	3
		Atlantic Panama and Texas	1.31-1.62	1.49	5
		Eastern Pacific	1.28-1.76	1.45	17
		All localities	1.28-2.04	1.56	31

Data on $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum and $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ are given in Table 37.

The smallest, seemingly free-living specimen seen by me was 312 mm long (from Brazil) and the largest embryo 340 mm (from Saigon). Of the very few literature reports giving data on size and reproduction in *porosus*, Sadowsky (1967a) recorded embryos from southern Brazil as being usually 370-390 mm long though the largest was 402 mm; the smallest free-living specimen he observed was 380 mm. Meek and Hildebrand (1923) referred to well-developed embryos from Pacific Panama of 310-330 mm. Baughman (1943— as *cerdale*) listed a female of 362 mm, presumably free-living, from Texas. Eastern Pacific males of 558 and 745 mm examined by me were immature, with clasper lengths of 2.2 and 2.7% TL; others from 780 mm (Surinam) to about 1,000 mm were mature, and one of these of 855 mm from the eastern Pacific had a clasper length of 9.4%. Gilbert in Jordan and Evermann (1898), when describing *cerdale* from Pacific Panama, noted that a male of 730 mm was immature whereas another of 850 mm was mature. The smallest mature male reported from southern Brazil by Sadowsky (1967a) was 766 mm. Cervigon (1968) recorded two mature males of 757 and 1,073 mm, with clasper lengths of 8.3 and 8.9% TL, from Venezuela. The only data on maturity in the female are from Sadowsky (1967a) who listed his smallest pregnant female as being 841 mm long; he also stated that the number of embryos per litter ranged from two to seven (mean five), and that young are born in the spring. A report by Menezes (1966) of 16 embryos supposedly from one female taken off Fortaleza, Brazil, does not appear referable to *porosus* Ranzani, for apart from the litter size appearing too large the embryos were stated to have from 134 to 163 vertebrae. Total vertebral counts of that magnitude would better fit *Rhizoprionodon porosus* Poey for which Springer (1964) gave a range of 136-159. The largest specimens seen by me were a female of 975 mm and a male of ca. 1,000 mm, both from the eastern Pacific, but these are clearly not of maximum size. The type of *porosus*, a male, described by Ranzani (1840) from Brazil was said to be 3 ft 10 in (ca. 1,170 mm) long. Sadowsky (1967a) recorded his largest Brazilian specimen, a female, as being 1,340 mm, and Cervigon (1968) indicated that none of his Venezuelan examples exceeded 1.5 m. In light of the above data, little credence can be placed on Herre's (1936) account of numerous specimens of 1.6-2.0 m being observed at the Galapagos, for not only do these seem to be unduly large but also there are no other reports to substantiate the presence of *porosus* at the Galapagos.

Distribution (see also Material examined).—*Carcharhinus porosus* is a coastal species occurring on both sides of tropical America and also, if my identifications of three Asian specimens are correct, represented in the tropical western Pacific by a form so similar that I am unable to regard it as specifically distinct. Suggestions that *porosus* occurs in the eastern Atlantic (based only on the poorly described *fissidens* Bennett (1831)) and the western Indian Ocean (based on one specimen reported by Fourmanoir (1961)) have little to support them; both are probably referable to *Rhizoprionodon acutus*.

The above distribution is, on zoogeographic grounds, unusual, to say the least, and is not matched in any other species of *Carcharhinus*. Decision as to whether it is only a fragment of a wider distribution (particularly for the Indo-Pacific) or a spurious one combining distinct American and Asian elements separable by criteria other than those used in the present study, will have to await further material and further study.

Differences in vertebral numbers between the populations of *porosus* on the two sides of the Central American isthmus and at differing latitudes in the western Atlantic (see p. 76) are striking but are based on relatively small samples from each locality, and will require the examination of more extensive material before the picture they present can be accepted with confidence. The underlying cause of the development of these seemingly discrete populations is likely to be complex, and contributed to not only by simple geographical separation but also water temperatures during early development of the embryos and ecological preferences which may lead to geographical isolation. With respect to the last of these, one clue may be provided by the observation of Springer (1950) that *porosus* prefers mud bottom near the mouths of large rivers.

Specimens examined by me cover most of the known distribution of *porosus*, but in the detailed ranges given below my records are supplemented by others from Bigelow and Schroeder (1948), Rosenblatt and Baldwin (1958), Lowe (McConnell) (1962), Sadowsky (1967a), and Cervigon (1968).

Western Atlantic from as far as about lat. 30°30' N (Mississippi) to lat. 24°59' S (Brazil, Cananéia) but not uniformly distributed between these limits and only along the continental coastlines, with no records from the offshore islands of the Caribbean. Within this broad range, known localities include the Gulf of Mexico at Mississippi (Biloxi) and Texas (Galveston); Atlantic Panama (Colon); eastern Venezuela (but not on the north coast or near Margarita Island or to the north of Trinidad according to Cervigon 1968); British Guiana, Surinam, and French Guiana (the latter at Cayenne); and Brazil at several wide-spaced localities covering much of the coastline from Marajo Island near the mouth of the Amazon in the north and southwards at Pernambuco, Bahia, Vitória, and Cananéia.

Eastern Pacific from Mexico (Gulf of California, San Felipe at lat. 31°03' N and San Blas at lat. 21°35' N), Pacific Panama, Colombia, Ecuador (Guayaquil), and Peru (Payta) at lat. 5°09' S. Herre's (1936) account of very large specimens far offshore at the Galapagos Islands cannot be confirmed.

Western North Pacific at Vietnam (Saigon), Thailand (Bangkok), and Borneo (Baram).

Material examined.—USNM 82707, seven embryos, five males, 282-317 mm, and two females, 303 and 308 mm, Panama, Chame Point, R. Tweedlie; SU 52760, female embryo, 293 mm, Brazil, Espirito Santo, Vitória; SU 52746, male, 312 mm, Brazil, Maranhão, Madre Deus; SU 12866, female, 329 mm (paratype of *Carcharhinus cerdale*) Panama, January-February 1896, C. H. Gilbert; ANSP 76859, female embryo, 340 mm, Indo-China, Saigon, December 1934, H. Rutherford; BMNH (uncat.), female, 345 mm, and male, 347 mm, South America, Schomburgh; USNM 196798, female, 351 mm, Texas, Galveston, 7-14 July 1940, J. L. Baughman; UZMK PO 685, male, 352 mm, Brazil, Cotinguiba (?), Hyom; USNM 88676, two males, 355 and 417 mm, Ecuador, Guayaquil, 1926, W. L. Schmitt; ANSP 77121, female, 365 mm (paratype of *Carcharhinus tephrodes*), Borneo, Baram, 1897, A. C. Harrison Jr. and H. M. Hiller; ISZZ 4462, male, 375 mm, Guiana, Schomburgh; USNM 79323, male, 380 mm, Panama, Colon Fish Market, 19 January 1911, S. E. Meek and S. F. Hildebrand; USNM 53511, male, 388 mm, Ecuador, P. O. Simons; BMNH 1938.11.18.5, male, 391 mm,

Ecuador, Guayas River, Webb; SU 9293, female, 413 mm, and male, 420 mm, Ecuador, Guayaquil, P. O. Simons; USMN 79298, female, 420 mm, Panama, Panama City Fish Market, 30 March 1911, S. E. Meek and S. F. Hildebrand; MNHN 1139, male, 420 mm [syntype of *Carcharias (Prionodon) henlei*], Brazil; MNHN 1140, male, 422 mm [syntype of *Carcharias (Prionodon) henlei*], French Guiana, Cayenne, Poiteau; USNM 50438, female, 429 mm, Panama, C. H. Gilbert; NMV 61-463, female, 433 mm, Siam, Bangkok; USNM 79302, male, 453 mm, Panama, Colon Fish Market, 20 May 1911, S. E. Meek and S. F. Hildebrand; CNHM 8157, female, 460 mm, Panama, Colon, S. E. Meek and S. F. Hildebrand; USNM 79317, female, 495 mm, Panama, Colon Fish Market, 11 March 1911, S. E. Meek and S. F. Hildebrand; USNM 79316, male, 500 mm, Panama, Colon Fish Market, 11 March 1911, S. E. Meek and S. F. Hildebrand; USNM 79300, male, 505 mm, Panama, Panama City Fish Market, 20 May 1911, S. E. Meek and S. F. Hildebrand; UZMK PO 684, female, 513 mm, Berlin Museum; ISZZ 4463, male, 525 mm, Brazil, Moricand; SU 12865, male, 527 mm (paratype of *Carcharinus cerdale*), Panama, January-February 1896, C. H. Gilbert; USNM 181339, two females, 532 and 541 mm, Mexico, Nayarit, San Blas, 5-6 February 1958, B. W. Walker and party; USNM 181336, two females, 554 and 572 mm, Mexico, Nayarit, San Blas, 5-6 February 1958, B. W. Walker and party; SU 11884, male, 558 mm (holotype of *Carcharhinus cerdale*), Panama, January-February 1896, C. H. Gilbert and party; USNM 79312, female, 581 mm, Panama, Panama City Fish Market, 7 February 1911, S. E. Meek and S. F. Hildebrand; SU 11886, female, 602 mm (paratype of *Carcharhinus cerdale*), Panama, January-February 1896, C. H. Gilbert; USNM 79286, female, 605 mm, Panama, Colon Fish Market, 20 May 1911, S. E. Meek and S. F. Hildebrand; USNM 79326, male, 610 mm, Panama, Panama City Fish Market, 12 March 1911, S. E. Meek and S. F. Hildebrand; NMV 61-465 and 61-358, male, 665 mm, and female, 975 mm, Panama, 1902, Jordan; BMNH 1903.5.15.339-40, two males, 675 and 863 mm (the latter mature) (possibly paratypes of *Carcharhinus cerdale*), Panama, D. S. Jordan; ISZZ 15791, male, 730 mm, and female, ca. 860 mm, Panama, Stanford University; MCZ 709, two males, 745 and 855 mm, and one female, 885 mm, Panama, July 1872, Hassler Expedition; USNM 156722, mature male, 780 mm, Surinam, 1 mi SE of Paramaraibo Light Ship, 5 June 1957, J. B. Higman on the *Coquette*; USNM 79293, mature male, 838 mm, Panama, Panama City Fish Market, 19 April 1911, S. E. Meek and S. F. Hildebrand; UCLA 58-128, female, 860 mm, Pacific Panama between Point Gorda and Point Gorita, 16 February 1958; SIO 48-58, head, tail, and fins of mature male, about 1,000 mm long, presumably from eastern Pacific; MNHN 50-22, specimen not sexed or measured, Colombia, Bogota Museum.

Carcharhinus fitzroyensis (Whitley, 1943)

Figures 38, 39

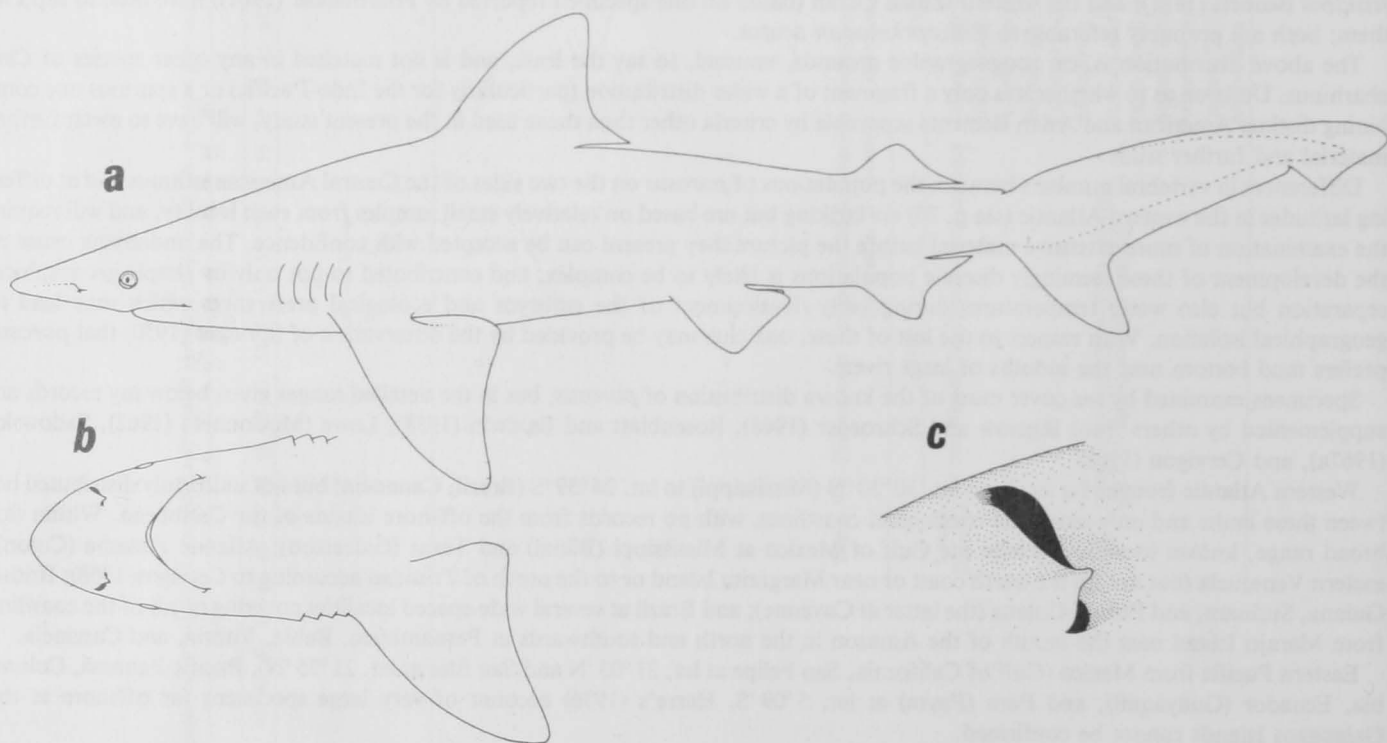


Figure 38.—*Carcharhinus fitzroyensis*, QMB I.7135, 735 mm TL, male from Queensland: a, left side; b, underside of head; c, enlarged left nostril.

Galeolamna (Uranganops) fitzroyensis Whitley, 1943:117-119, text fig. 2. Holotype, female, 1,174 mm; paratype, female, 743 mm; holotype from Connor's Creek, Fitzroy River estuary, Queensland, Australia; paratype from St. Crispin Reef, off Port Douglas, Queensland.

Diagnosis.—Moderate-sized sharks, probably up to 1.50 m long, lacking an interdorsal ridge; fins without obvious white or dark markings; snout long and pointed; internarial width 1.7-1.8 in preoral length; origin of first dorsal fin above inner pectoral corner or farther anterior over middle of inner pectoral margin; apex of first dorsal sharply rounded to pointed; origin of second dorsal above or slightly

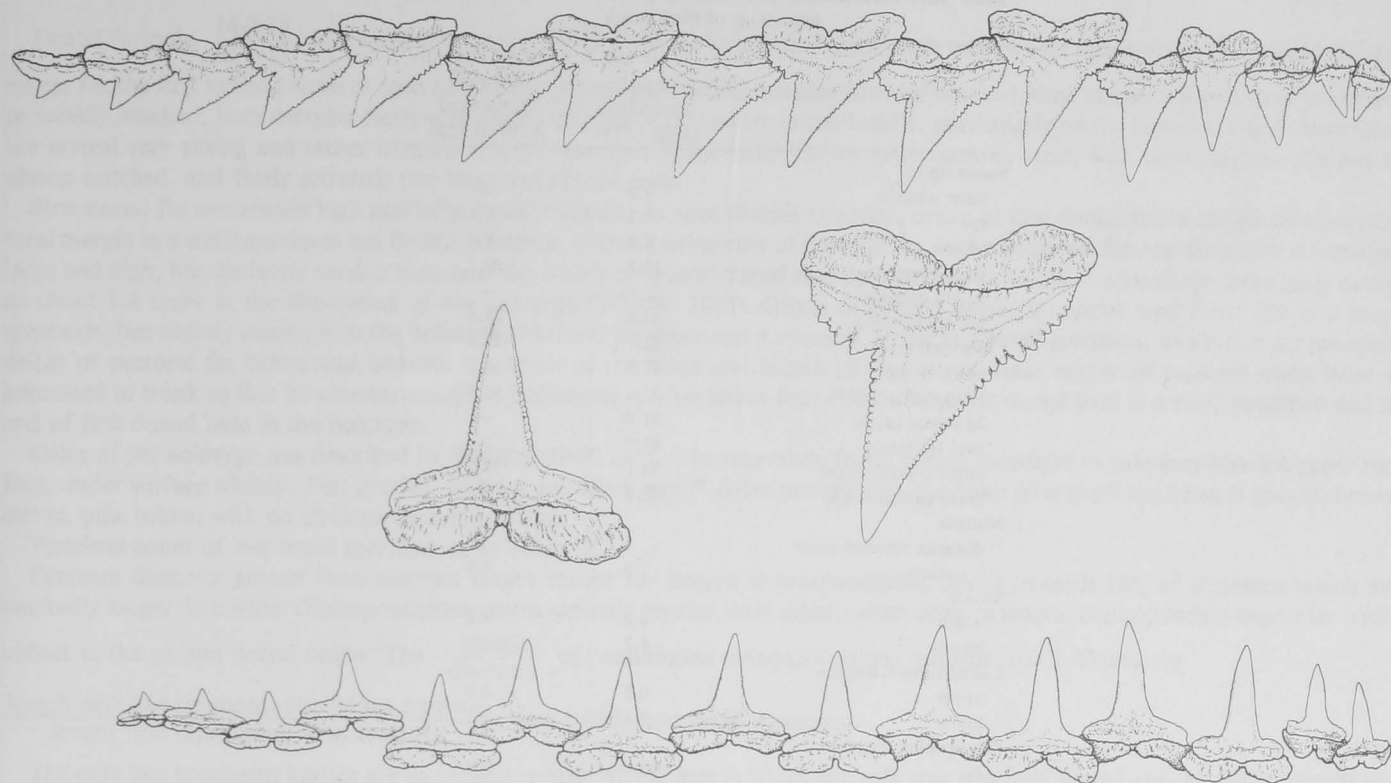


Figure 39.—*Carcharhinus fitzroyensis*, QMB I.7135, 735 mm TL, male from Queensland: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

behind anal fin origin; height of second dorsal 3.2% TL and 1.2 in length of its rear tip; dental formula $\frac{14-2-14}{13 \text{ or } 14-2-13 \text{ or } 14}$; upper teeth moderately narrow, oblique, deeply notched laterally, weakly notched to concave medially, with noticeably coarser serrations basally; lower teeth erect, serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 58; caudal centra 67; total centra 125; diplospondyly begins just in front of the second dorsal fin origin; diplospondylous centra alternating slightly in length; penultimate monospondylous centrum 1.4 times longer than wide.

The combination of a smooth back, no dark markings on any of the fins, a long pointed snout, and narrow, oblique upper teeth separates *fitzroyensis* from other Australian species, although attention to details of such features as tooth shape and pectoral fin length:width ratio is necessary when comparing it with juveniles of *brachyurus* and *brevipinna*. If *fitzroyensis* is found to have a wider Indo-west Pacific distribution it could be confused with species such as *porosus* and possibly *borneensis*, both of which, however, differ in having their second dorsal fin origin over or behind the middle of the anal fin base.

Nomenclatural discussion.—Whitley (1943:117) described *fitzroyensis* from one female specimen from Queensland, Australia, and listed but did not describe a smaller female paratype from another locality in Queensland. Only fragments of the holotype were preserved. I have examined these fragments (parts of the upper and lower jaws and a skin sample) in the Australian Museum (AMS IB 1229), together with the paratype (AMS IB 14569) which is complete, and conclude that they are different species. The paratype can be referred to *amblyrhynchus* Bleeker, 1856. No other specimens of *fitzroyensis* have been reported, but a juvenile specimen, 735 mm long, in the Queensland Museum (QMB I.7135), also collected from Queensland, agrees so well with the holotype of *fitzroyensis* that I can, with confidence, treat it as that species.

There are many similarities between *fitzroyensis* and an illustration of an Indonesian shark labelled as *Cynocephalus* (*Prionace*) *munising* Bleeker in an unpublished Bleeker Atlas in the Leiden Museum. However, apart from not being able to establish whether the illustrated specimen has any type status (see p. 188) I also note that the similarities are outweighed by important differences (particularly in eye size, position of first dorsal fin, and size of second dorsal relative to the anal fin) which rule out the likelihood of *munising* and *fitzroyensis* being conspecific.

Description (see also Table 38).—Maximum size not known, but probably not exceeding about 1.5 m TL. Midline of back smooth, lacking an interdorsal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles close-packed, overlapping, subcircular in outline, slightly wider than long, with three or occasionally five longitudinal ridges and three posterior marginal teeth.

Snout long and pointed in contour. Anterior margin of eye is slightly forward of front of mouth in a small specimen (735 mm TL) but was described as slightly behind front of mouth in the holotype. Nostrils oblique, with moderately ovate apertures, the anterior margin of each with an obvious, pointed lobe.

Table 38.—*Carcharhinus fitzroyensis*, proportional dimensions in percentage of total length.

	♂ 735 mm Australia Queensland QMB I 7135	♀ 1,174 mm Australia Queensland AMS IB 1229
Snout tip to		
outer nostrils	4.2	—
eye	7.7	9.3
mouth	8.3	8.6
1st gill opening	19.3	20.1
3d gill opening	21.6	—
5th gill opening	23.8	25.5
pectoral origin	22.7	22.8
pelvic origin	47.3	50.1
1st dorsal origin	31.1	33.7
2d dorsal origin	61.0	—
anal fin origin	61.0	—
upper caudal origin	73.1	73.5
lower caudal origin	72.1	—
Nostrils		
distance between inner corners	5.0	4.8
Mouth		
width	8.2	8.8
length	4.2	—
Labial furrow lengths		
upper	0.7	0.5
lower	0.4	0.3
Gill opening lengths		
1st	3.0	2.8
3d	3.0	—
5th	2.2	2.6
Eye		
horizontal diameter	1.4	1.4
1st dorsal fin		
length of base	10.5	10.9
length posterior margin	3.9	5.1
height	9.4	—
2d dorsal fin		
length of base	4.5	4.3
length posterior margin	3.8	4.1
height	3.2	—
Anal fin		
length of base	5.4	5.2
length posterior margin	3.4	3.8
height	4.2	—
Pectoral fin		
length of base	6.4	6.6
length anterior margin	17.1	19.1
length distal margin	13.9	—
greatest width	11.8	—
Pelvic fin		
length of base	5.7	—
length anterior margin	6.5	7.6
length distal margin	5.9	—
length of claspers	2.7	—
Caudal		
length of dorsal lobe	26.6	26.6
length of ventral lobe	11.0	11.6
Trunk at pectoral origin		
width	12.9	—
height	11.4	—
Dental formula	14-2-14 13-2-13	14-2-14 14-2-14
Vertebrae		
precaudal	58	—
caudal	67	—
total	125	—

♂ Holotype of *Galeolamna (Uranganops) fitzroyensis*. Measurements from Whitley 1943.

Dental formula $\frac{14-2-14}{13-2-13}$ in a small specimen, $\frac{14-2-14}{14-2-14}$ in the holotype. Upper teeth narrow and rather long, moderately oblique except for the first to third series at each side of symphysis, their lateral margins strongly notched, their medial margins mostly concave or weakly notched, both margins finely serrated distally but with coarser serrae basally, particularly on the lateral margin where there are several very strong and rather irregular serrae; two symphysial teeth. Lower teeth narrow, erect, with both margins concave to almost notched, and finely serrated; two large symphysial teeth.

First dorsal fin moderately high and long, weakly falcate, its apex sharply rounded; origin of first dorsal above middle of inner pectoral margin in a small specimen but farther posterior, above inner corner of pectoral fin, in the holotype. Second dorsal fin moderately large and high, but distinctly smaller than anal fin; length of second dorsal rear tip 1.2 times its height in a small specimen, and shown as about 1.4 times in the illustration of the holotype (Whitley 1943). Origin of second dorsal fin above anal fin origin in a small specimen, but slightly behind it in the holotype. Pectoral fin short and noticeably broad in a small specimen, its tip sharply rounded; origin of pectoral fin below and between the levels of the third and fourth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches about four-fifths along first dorsal base in a small specimen and to end of first dorsal base in the holotype.

Color of the holotype was described by Whitley (1943) as "... bronze when fresh, fading overnight to pale grey-blue on upper surface; under surface whitish. Fins greyish, without any black tips." After preservation the color of a small specimen is grayish-brown above, pale below, with no obvious dark-tipped fins.

Vertebral count of one small specimen as in Table 38.

Centrum diameter greater than centrum length except for longest monospondylous centra towards rear of abdomen which are markedly longer than wide. Diplospondylous centra virtually regular, only slightly alternating in length. Diplospondyly begins far back, almost at the second dorsal origin. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 1.40 and the

$\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.47 in one small specimen.

The only two specimens known are an immature male of 735 mm in which the yolk scar was fully healed and the clasper length was 2.7% TL, and the female holotype of 1,174 mm which was immature but approaching maturity since it contained ova up to 8 mm in diameter (Whitley 1943). On this slender evidence it is likely that *fitzroyensis* reaches a maximum size of 1.5 m or somewhat greater.

Distribution (see also Material examined).—So far known only from Queensland, Australia. The holotype was taken in the Fitzroy River estuary, southern Queensland, and the second specimen included in the present account was from Salamander Rocks, northern Queensland.

Material examined.—QMB I.7135, male, 735 mm, Australia, Queensland, Salamander Rocks, April 1941, G. Coates; AMS IB 1229, teeth and skin sample from female, 1,174 mm [holotype of *Galeolamna (Uranganops) fitzroyensis*], Australia, Queensland, Fitzroy River Estuary, Connor's Creek, 22 March 1943.

Carcharhinus leucas (Valenciennes in Müller and Henle, 1841)

Figures 40, 41

Carcharias (Prionodon) leucas Valenciennes in Müller and Henle, 1841:42-43. Four mounted specimens in the Paris Museum; measurements given of one of 6 ft 1 in 11 lines (1,878 mm); Antilles.

Carcharias (Prionodon) zambezensis Peters, 1852:276. Male, 760 mm, Zambezi River at Tette.

Squalus obtusus Poey, 1861:337-338, pl. 19, figs. 7, 8. Male, 2,300 mm, Cuba.

Squalus platyodon Poey, 1861:336-337, pl. 19, figs. 5, 6. Male, 2,500 mm, Cuba.

Eulamia nicaraguensis Gill and Bransford, 1877:190-191. Male, 6 ft 4 in (1,930 mm), Lake Nicaragua.

Carcharias azureus Gilbert and Starks, 1904:11-12, pl. 2, fig. 5. Two males and one female, 920-950 mm, Panama market.

Carcharias spenceri Ogilby, 1910:3-4. Holotype, 1,220 mm, Queensland, Brisbane River.

Galeolamna (Bogimba) bogimba Whitley, 1943:123-125, text fig. 5. Male, 2,544 mm, Queensland, Bogimbah.

Galeolamna greyi mckaili Whitley, 1945:2. Male, 806 mm, Western Australia, Swan River.

Galeolamna mckaili Whitley, 1951b:190. Based on same specimen used in describing the subspecies *Galeolamna greyi mckaili* above.

Carcharhinus Vanrooyeni Smith, 1958b:12-14, 28, 4 text figures. Holotype, 4 ft (1,219 mm) long, Zululand.

Carcharhinus leucas leucas Urist, 1962:984-986. Atlantic.

Carcharhinus leucas nicaraguensis Urist, 1962:984-986. Lake Nicaragua.

Diagnosis.—Large sharks, up to 3.24 m long, lacking an interdorsal ridge; tips of fins somewhat dusky, more so in juveniles than adults; snout very short and bluntly rounded; internarial width 0.7-1.0 in preoral length; origin of first dorsal fin usually over or just posterior to pectoral axil but exceptionally may be nearer to inner pectoral corner; apex of first dorsal sharply rounded to pointed; origin of second dorsal in front of origin of anal fin; height of second dorsal 2.9-4.6% TL and 0.7-1.0 in length of its rear tip; dental formula usually $\frac{13-1-13}{12-1-12}$; but may be $\frac{12 \text{ to } 14-1-12 \text{ to } 14}{12 \text{ or } 13-1 \text{ or } 2-12 \text{ or } 13}$ upper teeth broad, erect to slightly oblique, concave or shallowly

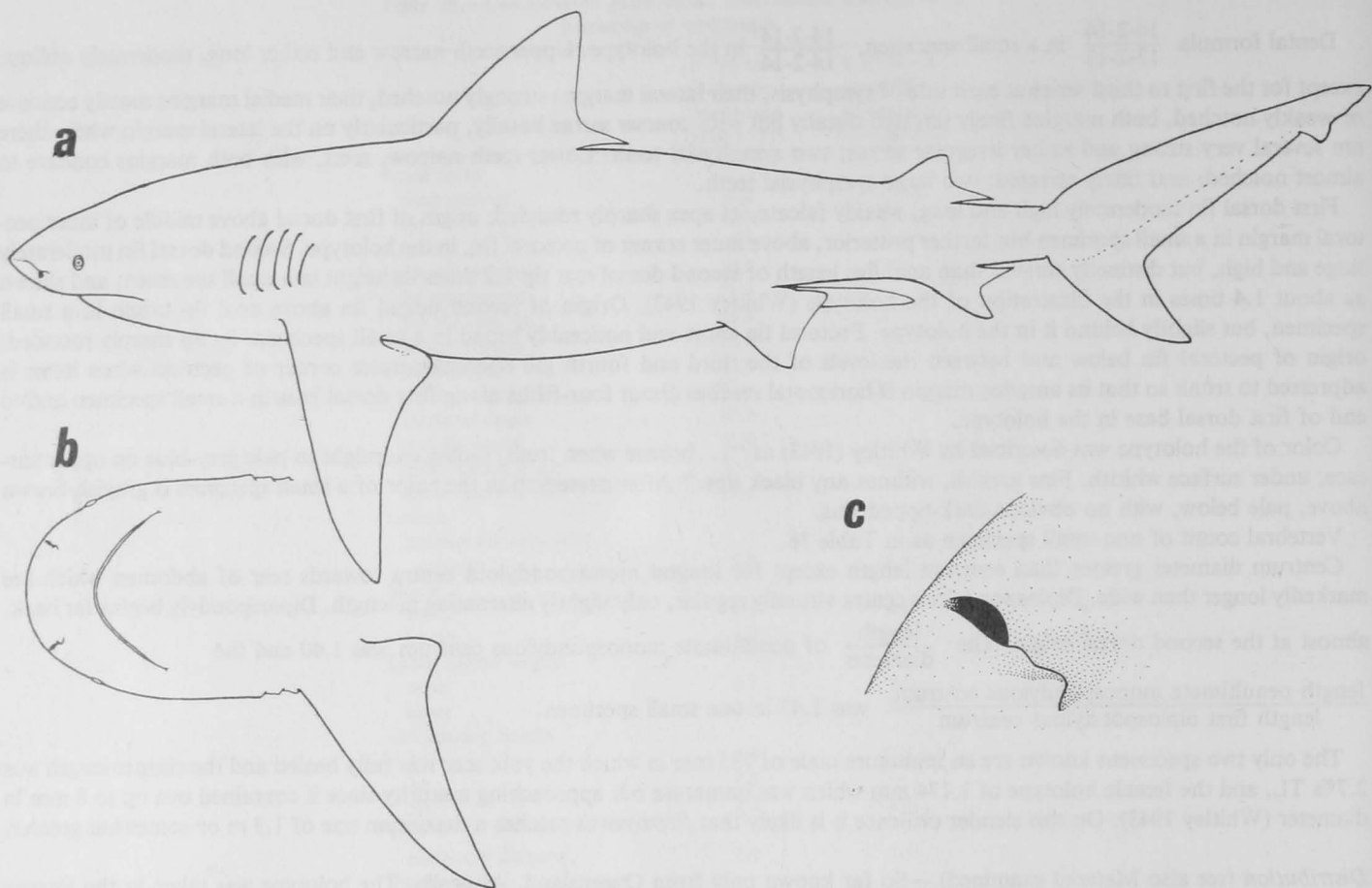


Figure 40.—*Carcharhinus leucas*, GVF 2353, 2,355 mm TL, male from Gulf of Thailand: a, left side; b, underside of head; c, enlarged left nostril. Note: The specimen figured is unusual in having the first dorsal origin almost over the pectoral inner corner rather than over the pectoral axil.

notched laterally, with slightly coarser serrations basally; lower teeth erect, serrated; no obvious discrete series of enlarged hyoman-dibular pores alongside corner of mouth; precaudal centra 101-123; caudal centra 93-104; total centra 198-227; diplospondyly begins one-third along pelvic base; diplospondylous centra regular in length; penultimate monospondylous centrum 1.4-1.7 times wider than long.

This species and *amboinensis* are the only smooth-backed *Carcharhinus* with a very short, bluntly rounded snout, broad, essentially erect upper teeth, and no obvious color pattern other than somewhat dusky fin tips. Although *leucas* and *amboinensis* are remarkably similar externally, they can nearly always be separated by the ratio of first dorsal height:second dorsal height (3.1 or less for *leucas*, more than 3.1 for *amboinensis*), and usually by the number of teeth on each side of the lower jaw (normally 12 but occasionally 13 in *leucas*, and 11 in *amboinensis*). Precaudal vertebral numbers provide the surest means of separating these two species, *leucas* having 101-123 and *amboinensis* only 89-95.

Nomenclatural discussion.—As indicated by the synonymy on p. 81, *leucas* has been a much described but poorly understood species. The two main reasons for this appear to be firstly, that it was not illustrated when initially described, and secondly, that its unusual propensity for living in water of low salinity led to the description of freshwater forms. Only recently has there been fairly general acceptance of the conspecificity of freshwater representatives, such as the Lake Nicaragua shark, with typical marine-dwelling *leucas*. The outstanding requirement that remains is to distinguish records of *leucas* from those of its sibling counterpart *amboinensis*. Differences between *leucas* and *amboinensis* are discussed on p. 92. Data supporting these differences, and at the same time substantiating the view that the nominal species here treated as *leucas* are in fact conspecific, are given in Table 39. Further comments on the nominal species are as follows.

Valenciennes' description (in Müller and Henle 1841) of *leucas* from the Antilles referred to four mounted specimens in the Paris Museum. Of these only two can now be found, a mature male (MNHN A9650) of 1,600 mm and a female (MNHN A9652) of 1,860 mm in which the tail tip is broken off. Presumably neither of these is the specimen for which Valenciennes gave measurements, as the latter, 6 ft 1 in 11 lines, would equal almost 2 m (assuming that Vienna inches and lines were used in Müller and Henle). However, these two syntypes are in good condition and are both clearly *leucas*. It is of interest to note that although the first dorsal fin origin is virtually above the pectoral axil in the larger syntype—hence in agreement with most descriptions of *leucas* from Atlantic specimens—it is farther back, above the middle of the inner (posterior) margin of the pectoral, in the smaller syntype. This latter situation is not uncommon in specimens of *leucas* from the Indo-Pacific but in the case of the syntype there is no way of knowing whether it was the condition in life or whether it was due to distortion of the skin at the time it was mounted.

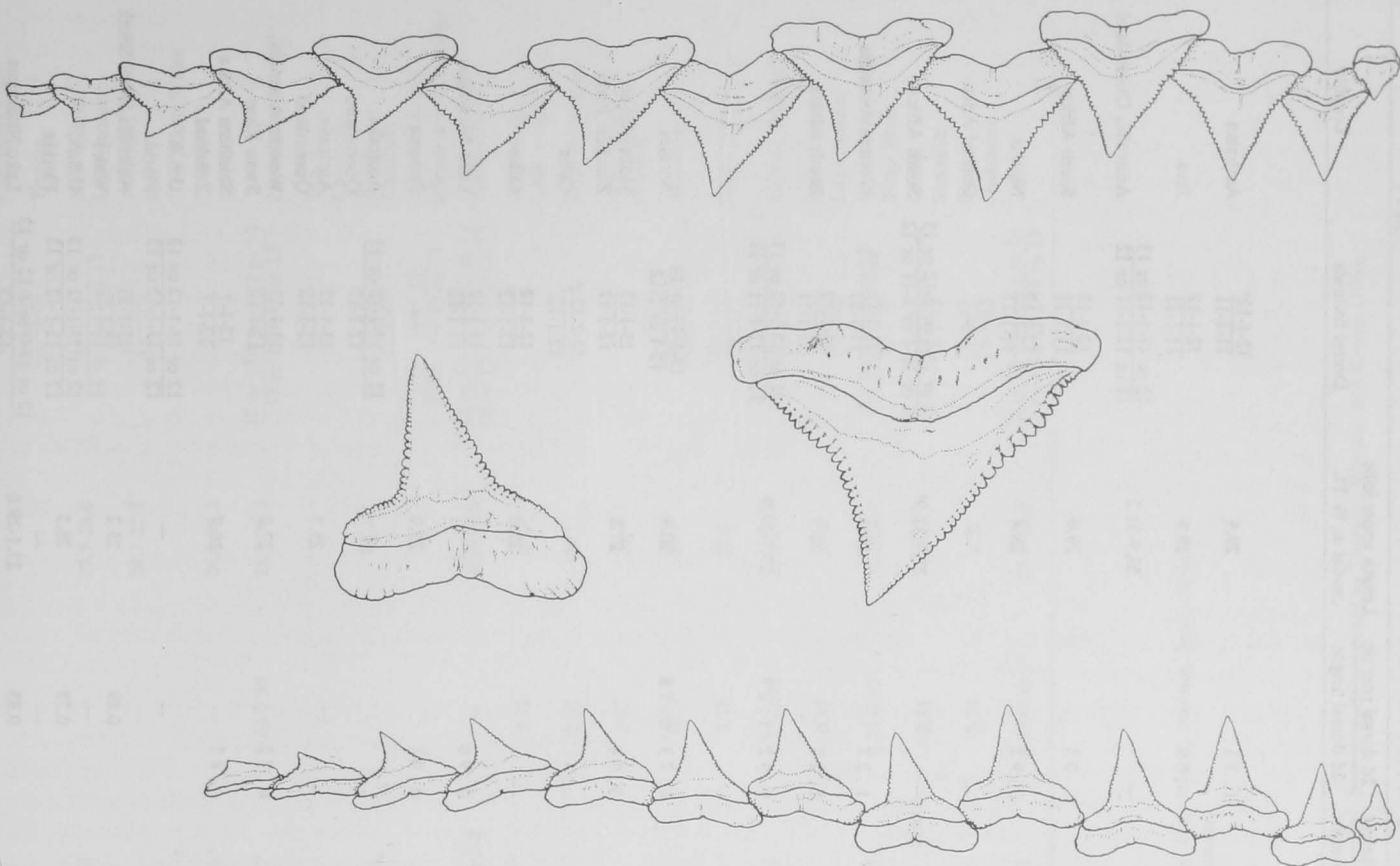


Figure 41.—*Carcharhinus leucas*, USNM 174073, from Australia, Northern Territory: right upper and lower teeth (symphysis to the right); inset teeth are fifth upper and lower teeth.

Peters' (1852:276) original account of *zambezensis* was nothing more than a very brief diagnosis together with a comment that his species had affinities with *leucas*. However his later account (1868:7) included a very adequate description plus measurements and excellent illustrations of the holotype, a male 735 mm long, taken in the Zambezi River about 120 mi from the coast, which was the only specimen Peters had. This specimen, still in the Berlin Museum (ISZZ 4468), agrees with *leucas* in all respects. Peters remarked that its presence in freshwater was notable and that despite its obvious similarity to *leucas* it differs in its slimmer form, color, and position of the anal fin—features which from my examination of the holotype I do not find significant.

Poey (1861:336) based his *platyodon* on a male specimen of 2,500 mm from Cuba. In the same account, on the following page, he described *obtusius* from a mounted specimen, also a male, of 2,300 mm from Cuba. Poey noted that although *obtusius* was very similar to *platyodon* there were some differences. These differences do not seem to be very important, and subsequently Poey himself (1868:447) synonymized *platyodon* with *obtusius*. I do not know if Poey's types are still in existence but judging by the descriptions of *platyodon* and *obtusius*, including the dental formula $\begin{pmatrix} 12-2-12 \\ 12-1-12 \end{pmatrix}$ of the former, and Poey's illustrations of the teeth of both, they can with confidence be assigned to *leucas*. As supporting evidence there is the fact that no specimen referable to *amboinensis* has yet been reported from the western Atlantic.

Gill and Bransford (1877:190), who described their *nicaraguensis* from a 1,930 mm male (USNM 16887) from Lake Nicaragua, stated that it was most closely related to *milberti*, and this view was maintained by several later authors. Bigelow and Schroeder (1948) correctly showed that its affinities were with *leucas* but retained it as a separate species because of minor differences in proportions and because "...it is the only shark that is known to have adapted itself permanently to life in fresh water." However in a later account (1961), when they had examined another specimen, they synonymized *nicaraguensis* with *leucas*. Urist (1962), who reported on the chemical composition of the blood and on calcium deposits in the skeleton of *nicaraguensis*, treated *nicaraguensis* as a subspecies of *leucas* but indicated that this referral was provisional. More recently Thorson, Watson, and Cowan (1966) in a valuable and substantive account of 19 specimens from two localities in Lake Nicaragua, one locality along the course of the Rio San Juan which connects Lake Nicaragua with the Caribbean and another at the mouth of this river, showed that comparison of their material with data on marine *leucas* from Bigelow and Schroeder (1948), Clark and von Schmidt (1965), and Schwartz (1959, 1960) gave no basis for regarding *nicaraguensis* as distinct from *leucas*. Nor could they find any significant difference between their material and specimens from Lake Jamoer, New Guinea, described and identified as *leucas* by Boeseman (1964). Thorson, Watson, and Cowan (1966) concluded from that study that the Lake Nicaragua sharks have an Atlantic origin, and that "there is no real basis for the belief that the shark population in the lake is landlocked." Subsequently Thorson (1971) demonstrated from tagging experiments that Lake Nicaragua sharks are not landlocked, and that the "Rio San Juan provides free passage to sharks in both directions for its full length." He noted, however, that "individual animals may stay in the lake for long periods of time."

Table 39.—Precaudal vertebral numbers, proportional dimensions, and dental formulae used in referring various nominal species to either *Carcharhinus amboinensis* or *C. leucas*.

	No. of specimens	Precaudal vertebrae	1st dorsal height 2d dorsal height	2d dorsal rear tip 2d dorsal height	Length upper lobe caudal as % TL	Dental formula	Locality
<i>Carcharhinus amboinensis</i>							
Nominal species ¹							
<i>Carcharias (Prionodon) amboinensis</i> Müller and Henle, 1841	1	—	3 . 7	1 . 1 1	29.6	$\frac{12-1-12^2}{11-1-11}$	Amboina
<i>Carcharias (Prionodon) henlei</i> ² Bleeker, 1853	1	—	3 . 1	1 . 0 9	29.6	$\frac{12-1-12}{11-1-11}$	Java
Descriptions by other authors							
<i>Galeolamna (Lamnarius) spenceri</i> : Whitley, 1943	4	—	—	—	28.9-31.2	$\frac{12 \text{ or } 13-1-12 \text{ or } 13}{11 \text{ or } 12-1-11 \text{ or } 12}$	Australia, Queensland
<i>Carcharinus zambezensis</i> : Smith, 1952(a)	1	—	3 . 6	1 . 0 3	29.0	$\frac{12-1-12}{11-1-11}$	South Africa
<i>Carcharhinus amboinensis</i> : Krefft, 1968	1	95	3 . 5	0 . 9 2	28.4	$\frac{12-1-12}{11-1-11}$	Nigeria
<i>Carcharhinus amboinensis</i> : D'Aubrey ⁴	1	89	—	—	—	—	Gulf of Aden
<i>Carcharhinus amboinensis</i> : Bass et al., 1973	Up to 41 ¹	90-95	3.2 or more—	—	27.7-32.9 ⁶	$\frac{12 \text{ or } 13-1 \text{ or } 2-12 \text{ or } 13}{11 \text{ or } 12-1 \text{ or } 2-11 \text{ or } 12}$	South Africa
<i>Carcharhinus amboinensis</i> : Bass ⁷	1	90	4 . 0	1 . 2 7	29.9	$\frac{11-1-11}{11-1-11}$	Western Australia
Specimen examined in present study							
ORID 567	1	94	3 . 7	1 . 2 7	28.9	$\frac{12-1-12}{11-1-11}$	South Africa
Range							
		89-95	3 . 1 - 3 . 7	0 . 9 2 - 1 . 2 7	27.7-32.9	$\frac{12 \text{ or } 13-1-12 \text{ or } 13}{11 \text{ or } 12-1-11 \text{ or } 12}$	
<i>Carcharhinus leucas</i>							
Nominal species ¹							
<i>Carcharias (Prionodon) leucas</i> Valenciennes in Müller and Henle, 1841	2	—	2 . 6	0 . 7 3 - 0 . 7 8	20.9	$\frac{13-1-13 \text{ or } 14}{12-1 \text{ or } 2-12}$	Antilles
<i>Carcharias (Prionodon) zambezensis</i> Peters 1852, 1868	1	—	2 . 4	0 . 9 4	27.8	$\frac{13-1-13}{12-1-12}$	Mozambique, Zambezi River
<i>Squalus obtusus</i> Poey, 1861	1	—	—	—	—	$\frac{12-2-12^2}{12-1-12^2}$	Cuba
<i>Squalus platyodon</i> Poey, 1861	1	—	—	—	25.0	$\frac{12-2-12}{12-1-12}$	Cuba
<i>Eulamia nicaraguensis</i> Gill and Bransford, 1877	1	—	3 . 0	0 . 9 0	—	$\frac{12-1-12}{12-1-12}$	Lake Nicaragua
<i>Carcharias azureus</i> Gilbert and Starks, 1904	1	114	2 . 1	0 . 7 3	27.9	—	Panama
<i>Carcharias spenceri</i> Ogilby, 1910	1	—	—	—	27.7 ⁸	$\frac{12 \text{ or } 13-1-12 \text{ or } 13}{12-1-12}$	Australia, Queensland
<i>Galeolamna (Bogimba) bogimba</i> Whitley, 1943	1	—	—	—	25.7	$\frac{13-1-12}{12-1-12}$	Australia, Queensland
<i>Galeolamna greyi mckaili</i> Whitley, 1940	1	—	2 . 4	0 . 7 7	27.2	$\frac{13-1-13}{12-1-12}$	Western Australia, Swan River
<i>Carcharhinus vanrooyeni</i> Smith, 1958a	1	—	2 . 4	0 . 8 3	26.7	$\frac{12-1-?}{12-1-?}$	Southern Africa Zululand
Descriptions by other authors							
<i>Carcharinus platyodon</i> : Springer 1939	17	—	—	—	—	$\frac{12 \text{ or } 13-1-12 \text{ or } 13}{12 \text{ or } 13-1-12 \text{ or } 13}$	U.S.A. Florida
<i>Galeolamna (Lamnarius) spenceri</i> : Whitley 1943	1	120	2.3	0.89	25.2	$\frac{13-1-13}{12-1-12}$	Australia, New South Wales
<i>Carcharhinus leucas</i> : Bigelow and Schroeder 1948	1	—	2.3	0.78	28.3	$\frac{12 \text{ or } 13-1-12 \text{ or } 13}{12 \text{ or } 13-1-12 \text{ or } 13}$	U.S.A. Florida
<i>Carcharhinus nicaraguensis</i> : Bigelow and Schroeder 1948	2	—	2.6	0.85	27.1-29.6	$\frac{12 \text{ or } 13-0 \text{ or } 1-12 \text{ or } 13}{12-1-12}$	Lake Nicaragua

<i>Carcharhinus leucas</i> : Schwartz 1960	24	—	—	—	—	$\frac{25 \text{ to } 29}{25 \text{ to } 27}$	Florida
<i>Carcharhinus leucas</i> : Boeseman 1964	3	—	2.4-2.6	—	27.5-28.0	$\frac{13-1-13}{11 \text{ to } 13-11 \text{ to } 13}$	New Guinea, Lake Jamoer
<i>Galeolamna (Bogimba) bogimba</i> : Whitley 1964	2	—	—	—	24.7-25.1	$\frac{13-1-13}{12-1-12}$	Australia, Queensland and New South Wales
<i>Carcharhinus leucas</i> : Clark and von Schmidt 1965	35	—	2.0-2.9 ¹⁰	—	24.0-30.3	—	U.S.A. Florida
<i>Carcharhinus leucas</i> : Thorson ¹¹	19	109-112	2.4-3.2	0.69-0.98	26.7-30.3	$\frac{12 \text{ or } 13-0 \text{ or } 1-12 \text{ or } 13}{12 \text{ or } 13-1-12 \text{ or } 13}$	Nicaragua
<i>Carcharhinus leucas</i> : Sadowsky 1967a	10	101-109	—	—	—	—	Brazil, Cananéia
<i>Carcharhinus leucas</i> : Sadowsky 1971	94	109-115 ¹²	2.3-3.1	—	—	$\frac{13-1-13^{13}}{12-1-12}$	Brazil, Cananéia
<i>Carcharhinus leucas</i> : Thorson 1972	5	—	—	—	—	$\frac{13-1-12 \text{ or } 13}{11 \text{ to } 13-1-11 \text{ to } 13}$	Amazon River, (Brazil and Colombia)
<i>Carcharhinus leucas</i> : Bass et al. 1973	up to 400 ¹⁴	112-123	Less than 3.2	—	25.0-30.0 ⁶	$\frac{12 \text{ or } 13-1 \text{ to } 3-12 \text{ or } 13}{12 \text{ or } 13-1 \text{ to } 3-12 \text{ or } 13}$	South Africa
Specimens examined in present study							
USNM 134326	1	110	2.7	0.78	27.9	—	Guatemala, Lake Yzabal
USNM 120372	1	—	2.7	0.93	29.1	—	Lake Nicaragua
MRAC 87417	1	—	2.2	0.87	26.4	—	West Africa, Banana
DIRU 9	1	—	2.2	0.77	27.1	$\frac{13-1-13}{12-1-12}$	Rhodesia
ORID 713	1	118	2.7	0.73	25.6	$\frac{13-1-13}{12-1-12}$	South Africa
GVF 2157, 2353	2	—	2.7-2.8	0.85-0.92	24.7-26.1	$\frac{13-1-13}{12-1-12}$	Gulf of Thailand
RNH 24611	1	119	2.3	0.87	27.9	$\frac{13-1-13}{12-1-12}$	New Guinea, Lake Jamoer
RNH 24612, 24271; WAM P.861	3	113-118	2.1-2.5	0.75-0.95	25.8-26.4	$\frac{12 \text{ or } 13-1-12 \text{ or } 13}{12-1-12}$	Western Australia, Swan River
BMNH 74.1.16.63	1	119	2.3	0.81	26.5	$\frac{13-1-13}{12-1-12}$	China, Shanghai
USNM 53528	1	—	—	0.79	28.8	$\frac{13-1-13}{13-1-13}$	Ecuador, Guayaquil
Range		101-123	2.0-3.5	0.69-0.99	20.9-30.3	$\frac{12 \text{ or } 13-0 \text{ to } 2-12 \text{ to } 14}{11 \text{ to } 13-0 \text{ to } 2-11 \text{ to } 13}$	

¹Data from original descriptions, supplemented in some cases with information from the types.

²Given as $\frac{25}{25}$ by Müller and Henle (1841) but there are not more than 23 teeth across the lower jaws.

³The name *henlei* Bleeker being preoccupied by *henlei* Valenciennes was later replaced by *brachyrhynchus* Bleeker.

⁴D'Aubrey, J. D. 1971. The taxonomy of two shark species of the genus *Carcharhinus*. Unpubl. M. Sc. Thesis, 171 p. Univ. Natal, Durban, South Africa.

⁵Of this number 16 specimens were cited for precaudal counts, 24 for proportional dimensions, and 26 for dental formulae.

⁶Presented here in a different format from that in Bass et al. (1973).

⁷J. Bass, Western Australian Museum, Beaufort St., Perth, pers. commun. July 1976.

⁸Based on the statement in Poey (1861) that the dental formula of *obtusius* is probably the same as in *platyodon*.

⁹Ogilby (1910) described the proportions in terms of "length of body" but it is clear that he meant total length.

¹⁰The range given here is based on averages of five size groups.

¹¹T. B. Thorson, Department of Zoology and Physiology, University of Nebraska, Lincoln, Nebr., pers. commun. July 1965. Subsequently published in Thorson, Watson, and Cowan (1966).

¹²Based on 27 specimens.

¹³Sadowsky notes that in six specimens there was an extra upper tooth, and in one specimen there were only 11 teeth on one side of the lower jaw.

¹⁴Of this number 92 specimens were cited for precaudal counts, 120 for proportional dimensions, and 136 for dental formulae.

The original description of *azureus* in Gilbert and Starks (1904:11) was based on three juvenile specimens, "92 to 95 cm," from the Panama market and hence presumably from the eastern Pacific. Gilbert and Starks noted that *azureus* was "extremely near *nicaraguensis*" but described it as a new species because "of the exceptional distribution of *C. nicaraguensis*, known only from fresh waters, which belong to the Atlantic slope. . . ." Their view on its affinity with *nicaraguensis* (= *leucas*) was amply supported by their description and excellent illustrations, but unfortunately the status of *azureus* was later confused by Garman's (1913) referral of it to *milberti*—an action subsequently supported by Meek and Hildebrand (1923). Likewise Beebe and Tee-Van (1941) noted that it "... is closely related to the Atlantic *Eulamia milberti*" and Bini and Tortonese (1955) suggested that it might be considered as a subspecies of *plumbeus*. A further complication in the literature was introduced by Rosenblatt and Baldwin's (1958) identification as *azureus* of a small embryo with a middorsal ridge, whereas *azureus* proper is smooth backed—this embryo is, in fact, a specimen of *albimarginatus*. Examination of the holotype of *azureus* in the Stanford Natural History Museum (SU 11890), and of what is probably a paratype in the British Museum (BMNH 1903.5.15.338), shows that both are definitely referable to *leucas*. The fate of the third type specimen mentioned by Gilbert and Starks is not known.

Ogilby (1910:3) described *spenceri* from a specimen 1,220 mm long from the Brisbane River, Queensland, Australia. The description agrees with *leucas*—but equally as well with *amboinensis*—in terms of the short blunt snout, the position of the anal fin relative to the second dorsal fin, and the teeth. Ogilby did not give details of dorsal fin heights, nor of the length of the rear tip of the second dorsal, and he did not illustrate *spenceri*. The holotype, said to be no. 290 in the collection of the Amateur Fishermen's Association of Queensland, cannot be found, and in any case comprised only the jaws. Both *leucas* and also, apparently, *amboinensis* occur in Queensland. Decision as to whether *spenceri* is *leucas* or *amboinensis* can, therefore, be made only on Ogilby's description that the dental formula was $\frac{12 \text{ or } 13-1-12 \text{ or } 13}{12-1-12}$, and that the "caudal" (presumably equivalent to the upper lobe of the caudal) was 3.6 in total length and hence equal to 27.7% TL. As can be seen from Tables 39 and 40 and my account of *amboinensis*, these data indicate a greater probability for *leucas* than they do for *amboinensis*. On this basis, and because nomenclature will not be affected by whatever decision is made, I choose to relegate *spenceri* to *leucas*.

The question of the identity of *bogimba*, described from a 2,544 mm male from Fraser Island, Queensland, by Whitley (1943:123) depends on essentially the same kind of data as are available for *spenceri*, except that Whitley illustrated his specimen and there are a few fragments (some teeth and a sample of skin) of the holotype preserved in the Australian Museum (AMS IB.1225). I have examined the latter and they agree with *leucas* and *amboinensis*, as does the description in general of *bogimba*. The principal disquieting feature is that the illustration of *bogimba* shows a second dorsal fin that is too small for either *leucas* or *amboinensis*. On the other hand, the shape of the first dorsal fin, the pectoral fin, and the lower lobe of the caudal are sufficiently unrealistic in the illustration to give an impression that the illustration was based on a rough field sketch or reconstructed from measurements and field notes. If this was the case then the apparent discrepancy in the size of the second dorsal fin may not be significant. The dental formula of $\frac{13-0-12}{12-1-12}$ (or $\frac{13-1-12}{12-1-12}$ if

Whitley's remark that there is a symphyseal tooth behind the functional series in the upper jaw is taken into account) together with the short upper lobe of the caudal fin (25.7% TL) suggest strongly that *leucas* was involved. Whitley compared *bogimba* only with the ridged-back *stevensi* (= *plumbeus*) which he redescribed in the same account. It might appear significant that he did not compare his smooth-back *bogimba* with the smooth-back *spenceri* (= *leucas*) which he also treated in the same account, but this was possibly because of an error on his part—in a footnote (p. 123) to his description of *bogimba* he pointed out the importance of the middorsal ridge as a taxonomic character and stated that a ridge is always present in both males and females of *spenceri*. However, a few pages before (p. 120) in his description of *spenceri* he noted, correctly, that *spenceri* lacks a middorsal ridge. In a later publication, Whitley (1964) reported another specimen of *bogimba* from Queensland and one from Sydney Harbor, but again although he gave many measurements he did not give the critical ones for the dorsal fins to allow an unequivocal decision as to whether *leucas* or *amboinensis* was involved. Only fragments of these specimens, including one complete set of jaws (AMS IB.6007), are preserved in the Australian Museum. The dental formula in both specimens was $\frac{13-1-13}{12-1-12}$ and the upper caudal lobe lengths were 24.7 and 25.1% TL. Whitley commented on this occasion (1964:159) that "*G. bogimba* is apparently not the adult of *spenceri* as the characters separating them are probably more than can be accounted for by growth." However, I have tested these characters (various proportional dimensions, etc.) which Whitley gave in a key immediately following his comment and I find that they are, indeed, quite accountable for by growth between juveniles and adults of *leucas*. For this reason, and again because nomenclature will not be affected and because the dental formulae and upper caudal lobe lengths give a greater probability that Whitley was dealing with *leucas* rather than with *amboinensis*, I assign *bogimba* to *leucas*.

The subspecies *Galeolamna greyi mckaili* was named and briefly diagnosed by Whitley (1945:2); reference was made to a small Western Australian specimen previously described and illustrated by Whitley (1940) as *G. greyi*, and this specimen was designated as holotype of the subspecies. Later (1951b:190) Whitley gave *mckaili* full specific status because he found it had a wider distribution in Western Australia, but he did not add any further significant data. I have examined the holotype of *mckaili* in the Australian Museum (IB.508) and found that it agrees with *leucas* in all respects (see Table 39). The question might well be asked why this specimen, 830 mm long, is superficially so different in appearance, at least as regards the shape of the first dorsal fin, from another of comparable size, 837 mm, from Lake Macquarie, New South Wales, which I also recognize as *leucas*. The latter specimen (AMS I.7586) was first illustrated in Waite (1906) as *brachyurus*, and this illustration was repeated in Whitley (1940) as *stevensi* and in Whitley (1943) as *spenceri*. The answer lies, I believe, in variation in birth size. The Western Australian specimen, although slightly smaller was clearly free living, and its first dorsal fin already had progressed from the low rounded-apex form of the late embryo to the more erect pointed-apex form of the juvenile. The New South Wales specimen still retains an open umbilical scar which, together with the embryonic shape of its first dorsal fin, suggests that despite its larger size it had not reached the same stage in development. If it was free living, which one would expect

Table 40.—*Carcharhinus leucas*, proportional dimensions in percentage of total length.

	♂ 728 mm West Africa Banana MRAC 37417	♂ 729 mm China Shanghai BMNH 74.	♀ 731 mm New Guinea Lake Jamoer RNH 24611	♂ 915 mm Panama SU 11890	♀ 915 mm Guatemala Lake Yzabal USNM 134326	♂ 1,085 mm Western Australia Swan River RNH 24271	♀ 1,125 mm Africa Zululand DIRU	♂ 1,782 mm Gulf of Thailand GVF 2157	♂ 2,355 mm Gulf of Thailand GVF 2358	♀ 2,770 mm South Africa Durban ORID 713
Snout tip to										
outer nostrils	2.6	2.5	2.5	2.0	2.1	1.9	2.0	1.7	1.7	1.8
eye	6.2	6.0	6.1	5.2	5.4	4.9	5.1	4.5	4.8	5.4
mouth	6.5	5.8	6.3	5.6	6.0	4.9	5.5	4.6	5.0	5.4
1st gill opening	18.3	—	17.8	17.7	17.6	17.1	17.5	15.9	17.1	17.3
3d gill opening	21.0	—	19.6	—	20.1	19.3	20.0	18.5	19.7	19.3
5th gill opening	23.1	21.4	21.6	20.8	22.5	21.1	21.4	20.4	21.5	21.3
pectoral origin	21.3	20.8	20.8	20.1	20.3	19.8	20.6	18.8	19.7	19.3
pelvic origin	49.4	49.5	49.2	46.5	48.4	50.0	51.5	49.4	51.8	53.0
1st dorsal origin	29.5	28.7	28.8	28.3	27.5	29.0	29.1	28.8	30.8	31.4
2d dorsal origin	61.0	61.0	59.5	59.6	60.3	61.4	62.1	61.4	64.7	63.1
anal fin origin	62.6	61.8	60.6	61.2	61.7	63.2	63.0	63.2	66.3	63.9
upper caudal origin	73.5	73.5	72.0	72.2	73.6	74.0	74.5	73.4	76.5	74.5
lower caudal origin	72.8	72.7	71.3	71.1	73.1	73.8	73.6	72.6	76.2	74.0
Nostrils										
distance between inner corners	6.9	6.6	6.5	6.5	6.8	6.3	6.3	5.9	6.3	6.5
Mouth										
width	9.4	9.2	8.6	10.1	9.3	9.1	—	9.9	11.5	11.3
length	5.0	4.5	4.6	4.7	4.2	4.7	5.1	4.7	5.1	4.7
Labial furrow lengths										
upper	0.5	0.5	0.5	0.7	—	—	—	—	0.4	0.4
lower	0.5	0.5	0.6	0.4	—	—	—	—	0.9	0.6
Gill opening lengths										
1st	2.9	—	3.0	3.3	3.2	3.3	3.3	3.4	4.2	4.4
3d	3.3	4.1	3.1	3.5	3.8	3.6	3.4	3.3	4.3	4.5
5th	2.5	—	2.2	2.3	2.8	2.9	2.1	2.1	2.9	3.3
Eye										
horizontal diameter	1.7	1.8	1.5	1.3	1.4	1.2	1.3	1.0	0.8	0.8
1st dorsal fin										
length of base	12.2	11.7	11.2	12.1	13.1	11.6	11.3	11.7	11.3	11.9
length posterior margin	3.0	3.2	2.9	3.3	3.5	3.5	3.6	3.6	3.5	3.1
height	7.0	8.3	8.2	9.5	10.8	9.2	9.2	9.5	9.9	10.3
2d dorsal fin										
length of base	5.3	5.2	5.5	5.6	5.7	5.4	4.9	4.7	4.8	5.0
length posterior margin	2.7	2.9	3.1	3.3	3.2	3.0	3.2	3.3	3.1	2.8
height	3.2	3.6	3.6	4.5	4.0	4.0	3.9	3.6	4.0	3.8
Anal fin										
length of base	5.0	5.1	5.3	5.1	5.5	5.1	5.0	4.7	4.7	4.8
length posterior margin	2.6	2.7	2.9	3.0	3.0	2.8	3.1	3.0	2.8	2.7
height	3.1	3.8	3.8	4.3	3.9	3.9	3.7	3.9	4.0	4.6
Pectoral fin										
length of base	7.0	6.9	6.3	7.1	7.2	7.2	7.3	7.3	7.6	7.9
length anterior margin	17.6	17.6	18.6	20.1	19.7	18.0	19.8	21.0	20.6	21.2
length distal margin	11.4	11.8	13.4	14.9	17.0	14.5	15.9	16.8	16.6	18.6
greatest width	9.3	9.6	9.8	11.4	11.9	10.1	11.0	11.2	11.0	11.4
Pelvic fin										
length of base	5.6	6.1	6.1	6.0	6.1	6.2	5.7	5.9	5.1	5.4
length anterior margin	6.1	6.4	7.0	7.1	7.2	6.4	7.5	7.3	6.4	7.0
length distal margin	5.5	5.8	6.1	6.5	7.1	6.8	6.3	6.2	6.4	6.8
length of claspers	1.9	2.1	—	2.2	—	1.9	—	1.6	8.8	—
Caudal										
length of upper lobe	26.4	26.5	27.9	27.9	27.9	26.3	26.7	26.1	24.7	25.6
length of lower lobe	10.8	11.6	12.3	12.4	12.3	—	12.1	12.9	12.5	12.0
Trunk at pectoral origin										
width	13.2	—	13.3	15.1	14.3	12.8	14.0	14.3	15.3	13.7
height	13.4	—	11.8	—	15.2	12.7	12.1	13.1	13.2	—
Dental formula	—	13-1-13 12-1-12	13-1-13 12-1-12	—	—	13-1-13 12-1-12	12-1-?	13-1-13 12-1-12	—	13-1-13 12-1-12
Vertebrae										
precaudal	—	119	119	114	110	118	—	—	—	118 ¹
caudal	—	100	—	104	99	—	—	—	—	102
total	—	219	—	218	209	—	—	—	—	220

¹Holotype of *Carcharias azureus*.²Holotype of *Carcharhinus vanrooyeni*.³Vertebral count supplied by J. D'Aubrey, Assistant Research Officer, Oceanographic Research Institute, 2 West St., Durban, pers. commun. July 1963.

from data on size at birth in *leucas* from other regions, then the time that had elapsed since its birth was less than that of the Western Australian specimen.

Smith (1958b:13) described *vanrooyeni* from Zululand in what is essentially a popular article in a sporting magazine. In consequence the description is meager and the diagnosis inadequate. Smith noted that *vanrooyeni* was related to *spenceri* (= *leucas*), *stevensi* (= *plumbeus*), the Zambezi shark (= *leucas*), and the Ganges shark (= *gangeticus*), but he did not give details. I have examined the holotype, a female of 1,125 mm in the Department of Ichthyology, Rhodes University, Grahamstown, and as shown here (Table 39) the dimensions of its dorsal fins and its dental formula establish it as *leucas*.

Description (see also Table 40).—Large sharks, growing to at least 3.2 m TL. Midline of back between dorsal fins smooth, lacking an interdorsal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles rather large, loose spaced in small specimens but close-packed and overlapping in larger, ovoid, each with three strong longitudinal ridges and corresponding sharp-pointed and strong posterior marginal teeth in small specimens, five to seven in larger ones.

Snout very short and bluntly rounded in contour. Anterior margin of eye above or more usually slightly forward of front of mouth. Nostrils strongly oblique, with broadly ovate apertures, the anterior margin of each with a low, blunt lobe.

Dental formula $\frac{13-1-13}{12-1-12}$ in 15 of 25 specimens counted; $\frac{12-1-12}{12-1-12}$ in 3; $\frac{12 \text{ or } 13-1-12 \text{ or } 13}{12 \text{ or } 13-1 \text{ or } 2-12 \text{ or } 13}$ in 5; and $\frac{13 \text{ or } 14-1-13 \text{ or } 14}{12 \text{ or } 13-1 \text{ or } 2-12 \text{ or } 13}$ in 2. Upper teeth broad, oblique except for first two series at front of mouth which are erect and symmetrical

with weakly concave margins; teeth further out along jaw with lateral margins concave or very shallowly notched, medial margins weakly convex, both margins serrated, the serrations of moderate size but somewhat coarser basally; one small symphyseal tooth. Lower teeth narrow, erect except for the most lateral three or four series on each side which are slightly oblique, both margins concave to notched basally but very slightly convex distally, serrated, the serrations finer than those of upper teeth; one or occasionally two small symphyseal teeth.

First dorsal fin moderately high and rather long based, its apex sharply rounded to pointed; origin of first dorsal over or just behind axil of pectoral in most specimens but farther back in some (particularly from the Indian Ocean and Indo-Australian region) and exceptionally almost as far back as the inner (posterior) corner of the pectoral fin. Second dorsal fin large and high, almost or quite equal to anal fin; length of second dorsal rear tip 0.73-0.95 (mean 0.82) times second dorsal height in 15 specimens; origin of second dorsal anterior to anal fin origin by a distance up to about one-third of anal base. Pectoral fins broad based, moderately long, slightly falcate; origin of pectorals below the third gill openings or below and between the levels of the third and fourth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches almost or quite to first dorsal axil in most specimens, and exceptionally slightly behind this level.

Color in life was described by Kato (1964—as *azureus*) as “Colour of dorsal surface brownish-gray, sometimes with tiny blue spots; sides light gray; ventral surface yellowish-white; undersides of pectoral and pelvic fin tips white to dusky.”

After preservation in alcohol the color is bluish, gray or brownish above, paler to white below; small specimens have a pale horizontal flank streak extending from above the pelvis forward along the midlevel of the body to the first dorsal, but this is not evident on subadults and adults. Small specimens also have dusky or black margins or tips on some or all of the fins; these markings are least developed on the first dorsal and pelvic fins. In the adults only faint dusky is evident, if at all, on the distal third of the underside of the pectoral, on the margins of the second dorsal fin and the dorsal lobe of the caudal, and on the tip of the ventral caudal lobe.

Vertebral counts of six specimens are given in Table 40 and of another 53 specimens in Table 41. Counts from 92 specimens from Natal, South Africa, given by Bass et al. (1973) had a precaudal range of 112-123 (mean 119.9) and a total range of 214-227 (mean 219.7).

Examination of the above counts on a regional basis (Table 42) strengthens Bass et al.'s (1973) statement that western Atlantic *leucas* have lower counts than those from the southwest Indian Ocean, and, for that matter, from the Indo-Australian region and the Persian Gulf.

Centrum diameter noticeably greater than centrum length even in longest monospondylous centra at posterior of abdomen. Diplospondylous centrum length regular. Diplospondyly begins above anterior third of pelvic base. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.58-0.70 (mean 0.62) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.10-1.42 (mean 1.22) in 10 specimens.

The smallest, definitely free-living specimen I have seen was 731 mm TL (from Lake Jamoer, New Guinea), while the largest embryo was 732 mm (from Swan River, Western Australia). Bigelow and Schroeder (1948) suggested that western Atlantic *leucas* were born at 650-700 mm, a size which Clark and von Schmidt (1965) considered was underestimated; the latter authors proposed a birth size of 740-750 mm and possibly somewhat larger for their Florida material. Sadowsky (1967a) reported embryos up to 765 mm from southern Brazil, and later (1971) documented others of 768-812 mm from the same locality. However, Thorson, Cowan, and Watson (1973) found free-living specimens of 560-720 mm in their Nicaragua material, having earlier (1966) reported two others of 694 and 701 mm from Guatemala. The extensive collection of *leucas* from South Africa studied by Bass et al. (1973) led them to report that size at birth was from 600 to 700 mm.

Data on maturity in the male as evidenced by clasper size is shown in Table 43 where the smallest mature male (from Lake Nicaragua) is 1,565 mm long and the largest immature male (from Florida) about 2,260 mm. Such variation has previously been noted by Thorson, Watson, and Cowan (1966). Bass et al. (1973) estimated the onset of maturity at about 2,240 mm in South African specimens.

The few definite data available on reproduction in the female are given in Table 44.

Table 41.—Vertebral numbers in 53 specimens of *Carcharhinus leucas*.

Specimens		Precaudal	Caudal	Total
USNM 196525	Florida ¹	112	98	210
USNM 196525	Florida ¹	111	97	208
USNM 196525	Florida ¹	110	98	208
SU 12216	Mexico, Tampico	114	101	215
	Guatemala ²	111	95	206
	Guatemala			
	Lake Yzabal ²	109	95	204
USNM 120371	Lake Nicaragua, San Carlos	113	95	208
	Lake Nicaragua, San Carlos ²	112	98	210
	Nicaragua, San Juan del Norte ²	111	96	207
	Lake Nicaragua, San Carlos ²	110	93	203
	Brazil, Cananéia ³			
	10 specimens	101-109 (mean 103)	—	198-208 (mean 201)
	Brazil, Cananéia ⁴			
	27 specimens	109-115 (mean 113)	—	
BMNH 94.8.3.72	Borneo, Sarawak	117	100	217
AMS 1.7586	Australia, New South Wales	120	—	—
BMNH 1846.9.11.118	Australia ⁵	118	99	217
BMNH 1953.5.10.6	Australia ⁵	117	98 +	215 +
WAM P.861	Western Australia, Swan River	118	101	219
RNH 24612	Western Australia, Swan River	113	—	—
Range (including counts from Table 40)		101-120	93-104	198-220

¹Sibling embryos.²Counts supplied by T. B. Thorson, Department of Zoology and Physiology, University of Nebraska, Lincoln, Nebr., pers. commun. July 1965.³Counts from Sadowsky (1967a).⁴Counts from Sadowsky (1971).⁵Probable syntypes of *Carcharias brachyurus*, and if so are most likely from Sydney, New South Wales (see p. 174).Table 42.—Precaudal vertebral numbers in *Carcharhinus leucas* from different localities.

Locality	No. of vertebrae		No. of specimens
	Range	Mean	
Western Atlantic	101-115	110.5	48
Southwest Indian Ocean	112-123	119.9	92
Indo-Australian region (including China)	113-120	117.8	9
Persian Gulf (Iraq)	115-119	117	2
Eastern Pacific	114	114	1

Table 43.—Clasper length as percentage of total length in *Carcharhinus leucas*.

Total length (mm)	Clasper length as %TL	Locality	Total length (mm)	Clasper length as %TL	Locality	Total length (mm)	Clasper length as %TL	Locality
728	1.9	West Africa	1,475	2.1	Nicaragua, ³ San Juan del Norte	1,800	3.0	Florida ¹
729	2.1	Shanghai	1,490	1.9	New Guinea, Lake Jamoer	1,852	9.2	Lake Nicaragua ³
732	1.7	Western Australia	1,565	10.9	Lake Nicaragua	1,930	10.9	Lake Nicaragua ³
797	2.0	Western Australia	1,584	3.1	Nicaragua, ³ Rio San Juan	1,950	3.2	Florida ¹
900	2.2	Florida ¹	1,600	8.1	Antilles ⁴	2,100	5.1	Florida ^{1,5,6}
915	2.2	Panama ²	1,650	2.1	Florida ¹	2,250	11.1	Virginia
1,085	1.9	Western Australia	1,740	9.4	Lake Nicaragua ³	2,250	7.8	Florida ^{1,5,6}
1,220	2.4	Lake Nicaragua ³	1,782	1.6	Gulf of Thailand	2,355	8.8	Gulf of Thailand
1,425	2.4	New Guinea, Lake Jamoer	1,800	10.2	Lake Nicaragua	2,400	8.1	Florida ¹

¹Data from Clark and von Schmidt (1965); where more than one specimen is listed the clasper lengths are averages and the total lengths are rounded to the nearest 150 mm.²Holotype of *Carcharias azureus*.³Data from Thorson, Watson, and Cowan (1966).⁴Syntype of *Carcharias (Prionodon) leucas*.⁵Holotype of *Eulamia nicaraguensis*.⁶Includes immature and mature individuals.

Table 44.—Size of pregnant females, number of embryos per litter, and size of embryos in *Carcharhinus leucas*.

Total length of mother (mm)	No. of embryos per litter	Total lengths of embryos (mm)	Date	Locality	Source
1,810	5	580 (mean)	June, July, and August	Costa Rica	Thorson and Gerst 1972
2,010	4	673 (mean)		Costa Rica	Thorson and Gerst 1972
2,020	3	623 (mean)		Costa Rica	Thorson and Gerst 1972
2,070	5	630 (mean)		Costa Rica	Thorson and Gerst 1972
2,100	5	570 (mean)		Costa Rica	Thorson and Gerst 1972
2,270	7	700 (mean)		Costa Rica	Thorson and Gerst 1972
2,280	6	651 (mean)		Costa Rica	Thorson and Gerst 1972
2,330	6	660-685	12 May	Florida	Clark and von Schmidt 1965
2,389	6	520-550	August	Brazil	Sadowsky 1967a
2,490	5	363-393	27 October	Florida	Clark and von Schmidt 1965
2,540	3 +	676-740	20 May	Florida	Clark and von Schmidt 1965
2,570	10	735-750	30 April	Florida	Clark and von Schmidt 1965
2,720	9	768-807	16 December	Brazil	Sadowsky 1971
2,750	10				
and longer	12	530-620	June	South Africa	Bass et al. 1973
(4 specimens)	12	680	November		
	12 or 13				
2,755	7	792-812	2 December	Brazil	Sadowsky 1971
3,240	4	728-765	February	Brazil	Sadowsky 1967a

The largest specimen of either sex that I have seen was a female of 2,770 mm from Durban. Various accounts in the literature suggest that *leucas* grows to 3,000 mm, while Kato et al. (1967) indicated a maximum of 3,400 mm. There are very few definite records which approach these suggested maxima, but Bass et al. (1973) recorded males and females up to 2,990 mm and 3,000 mm, respectively, from South Africa, while Sadowsky (1967a) listed a female of 3,240 mm from Brazil.

Distribution (see also Material examined).—Localities for the specimens of *leucas* that I have examined indicate that it is a worldwide species, principally of the tropical-subtropical regions but extending also into temperate waters. It is essentially an inshore species, and is frequently found in brackish water or even in freshwater in rivers and lakes (Boeseman 1964; Thorson, Watson, and Cowan 1966; Bass et al. 1973). Its occurrence in water of low salinity can, in many but not all cases, be associated with an inshore movement of the females for parturition; subsequently juveniles, and larger but immature sharks, may spend considerable periods in brackish water (Bass et al. 1973). The last-mentioned authors have also demonstrated that "... *leucas* can withstand a certain amount of hypersalinity but moves out of areas where the salinity is higher than about 50‰." Whether *leucas* is permanently resident in any freshwater localities remains to be determined.

There is an extensive literature on *leucas* and the nominal species here treated (p. 84) as conspecific with *leucas*. However, many of the reports under these names cannot be taken at face value because of confusion with other species. Conversely, as evidenced by the synonymy of *leucas* for the Atlantic in Bigelow and Schroeder (1948), *leucas* itself has frequently been misidentified and reported under different names. A similar situation pertains for the literature dealing with the Indian and Pacific Oceans, where, in particular, there has been notable confusion between *leucas* and the superficially similar but generically distinct *gangeticus*. Likewise the very close similarity between *leucas* and its sibling *amboinensis*, which two species are sympatric in some regions, provides added difficulties in interpreting the literature in many cases. Because of this situation, the detailed distribution given below reflects only to a limited degree the nominal literature, and is based mainly on specimens that I have seen together with information from Beebe and Tee-Van (1941 as *azureus*), Bigelow and Schroeder (1948), Schwartz (1960), Springer (1960), Lowe (McConnell) (1962), Boeseman (1964), Thorson, Watson, and Cowan (1966), Kato et al. (1967), Sadowsky (1967a, 1971), Thorson (1972), and Bass et al. (1973).

Western Atlantic from Massachusetts in the north, where *leucas* is an infrequent visitor, to southern Brazil (Cananéia), but seemingly most abundant in the Gulf of Mexico and the Caribbean area generally; for detailed accounts of its distribution in these areas see Bigelow and Schroeder (1948), Schwartz (1960), and Springer (1960). Eastern Atlantic from Senegal and southwards to at least Banana, Congo (lat. 6°S). Indian Ocean from Somalia and south to at least Durban and Algoa Bay in the west, and also from the River Tigris and the River Shatt-el-Arab in Iraq in the north. I have seen no specimens from India but it is likely that some, at least, of the reports from that region and elsewhere in the northern Indian Ocean were based on *leucas*. Indo-Australian region from the Gulf of Thailand, Borneo, New Guinea, and Australia (Western Australia, Northern Territory, Queensland, and New South Wales). Pacific Ocean from China (Shanghai) in the northwest, and from southern Baja California and the Gulf of California southward to at least Ecuador in the east. Kato et al. (1967) noted that *leucas* also occasionally wanders north to southern California, and Bini and Tortonese (1955) reported it (as *azureus*) from Peru.

There is no firm evidence for the presence of *leucas* in the Mediterranean, and I follow Bigelow and Schroeder (1948) and Tortonese (1951b) in discounting an early record under that name from Algeria—Tortonese's view that this was based on *plumbeus* is doubtless correct.

The occurrence of *leucas* in brackish water or freshwater was summarized by Bigelow and Schroeder (1948) for various localities communicating with the Atlantic Ocean (Louisiana, Atchafalaya River; Guatemala, Lake Yzabal; Honduras, Patuca River; Panama Canal, Miraflores Locks), while Myers (1952) reported what appears to be this shark from the Peruvian Amazon, 2,300 miles (about 4,000 km) upriver from the sea. More recently Thorson (1972) documented numerous occurrences of *leucas* in the Amazon, based on the examination of jaws from specimens taken up to 3,480 km upriver, and a verbal record for a locality 4,200 km upriver. Thomerson

and Thorson (1977) gave evidence for the capture of one specimen in 1937 from about 2,800 km upriver in the Mississippi at Alton, Ill. Schwartz (1960) commented on its occurrence in Chesapeake Bay, Thorson, Watson, and Cowan (1966) convincingly substantiated that the Lake Nicaragua shark formerly known as *nicaraguensis* is, in fact, *leucas*, and Boeseman (1964) gave an account of *leucas* from Lake Jamoer, New Guinea, and reviewed many of the above occurrences plus others, including different species, from freshwater in all parts of the world. Bass et al. (1973) tabulated records of *leucas* from rivers and lakes along the east coast of southern Africa, and provided extensive evidence on *leucas*' usage of Lake St. Lucia. Boeseman (1964) commented in his review, based mainly on literature up to 1948, "...that the recorded identifications do not always seem reliable..."—a view with which I agree in regard to many Indian and Pacific Ocean records. My data support the Atlantic occurrences noted above, and confirm records for the following localities: equatorial West Africa, Ogowe River; Iraq, Tigris River near Baghdad; Mozambique, Zambezi River near Tette; Rhodesia, Ruenwa River; New Guinea, Lake Jamoer; Western Australia, Swan River; Australia, Northern Territory, East Alligator River at Cahill's Landing; Australia, Queensland, Brisbane River, Herbert River; Australia, New South Wales, Lake Macquarie.

Material examined.—BMNH 1953.5.10.6, male embryo, 305 mm (probably a syntype of *Carcharias brachyurus*), Australia; BMNH 1846.9.11.118, male embryo, 496 mm (probably a syntype of *Carcharias brachyurus*), Australia, J. B. Jukes; NMV 61-418, male embryo, 665 mm, Brazil, Pará, 1904; IFAN 56-135, male embryo, 680 mm, Senegal, Joal, 9 April 1956, J. Cadenat; IFAN 56-136, female embryo, 680 mm, Senegal, Joal, 9 April 1956, J. Cadenat; USNM 196525, three male and female sibling embryos, ca. 690-715 mm, Florida, Miami, 17 May 1961, Staff of Miami Seaquarium; MRAC 87417, male embryo, 728 mm, West Africa, Banana, 1953, Major Marée; BMNH 74.1.16.63, male, 729 mm, China, Shanghai, R. Swinhoe; RNH 24611, female, 731 mm, New Guinea, Lake Jamoer, 24 March 1958; RNH 24612, male embryo, 732 mm, Western Australia, Swan River, Crawley Bay, 4 January 1960; ISZZ 4468, male, 735 mm [holotype of *Carcharias (Prionodon) zambezensis*], Zambezi River at Tette, W. Peters; DIRU, female, 738 mm, Rhodesia, Ruenwa River, B. Hill; SU 12216, female, 743 mm, Mexico, Tampico, J. O. Snyder; MSNG C.E. 36928, female, 745 mm, Somalia, Dolo, 1957; WAM P.793, female, 750 mm, Western Australia, Swan River near Narrows Bridge, 25 January 1960, B. B. Gardner; AMS I.3414, male, ca. 770 mm, Australia, Queensland, Herbert River, 1895, J. A. Boyd; BMNH 94.8.3.72, male, ca. 780 mm, Borneo, Sarawak, C. Hose; WAM P.861, male, 797 mm, Western Australia, Swan River, 6 January 1960, J. Bramley; NMV 61-427, male, 820 mm, Massachusetts, 1874; BMNH 1913.7.12.1, skin of male, ca. 820 mm, equatorial West Africa, Ogowe River, G. Schneider; AMS IB.508, male, 830 mm (holotype of the subspecies *Galeolamna greyi mckaili*), Western Australia, Swan River, L. Glauert; WAM P.882, male, 835 mm, Western Australia, Swan River, Pelican Point, 7 March 1960, W. E. Squires; AMS I.7586, female, 837 mm, Australia, New South Wales, Lake Macquarie, December 1905-January 1906; BMNH 1903.5.15.338, female, 900 mm (probably a paratype of *Carcharias azureus*), Panama, D. S. Jordan; SU 11890, male, 915 mm (holotype of *Carcharias azureus*), Panama Fish Market, January-February 1896, C. H. Gilbert and party; USNM 134326, female, 915 mm, Guatemala, Lake Yzabal, near northeast drainage (Atlantic), 7 April 1946, R. R. Miller; USNM 146541, male, 940 mm, Guatemala, Lake Yzabal, April 1947, R. R. Miller and party; UCLA 58-23, head and fins of female, ca. 1,000 mm, Mexico, San Blas, 1 February 1958, R. Rosenblatt; USNM 53528, skin of immature male, ca. 1,025 mm, Ecuador, Guayaquil, R. V. Anderson; RNH 24271, male, 1,085 mm, Western Australia, Swan River, east end of causeway, East Perth, 6 February 1961; USNM 127134, skin of female, ca. 1,100 mm, Panama Canal Zone, Miraflores Locks, 28-29 April 1937, A. O. Foster; DIRU, female, 1,125 mm (holotype of *Carcharhinus vanrooyeni*), Zululand; BMNH 1924.10.1.1, head of specimen 1,244 mm, River Tigris at Karrada, near Baghdad; USNM 146542, female, 1,270 mm, Guatemala, Lake Yzabal, Arena Chapin, 27 April 1947, R. R. Miller and party; USNM 120371, male, ca. 1,330 mm, Lake Nicaragua off San Carlos, August 1943, L. Marden; RNH 24699, partly skinned-out male, ca. 1,425 mm, New Guinea, Lake Jamoer, 22 March 1955; RNH 24698, male, ca. 1,490 mm, New Guinea, Lake Jamoer, 11 December 1954; MNHN A 9650, mounted skin of mature male, 1,600 mm [syntype of *Carcharias (Prionodon) leucas*], Puerto Rico; USNM 120372, mature male, ca. 1,620 mm, Lake Nicaragua, off San Carlos, September 1943, L. Marden; GVF 2157, immature male, 1,782 mm, Gulf of Thailand, Chumphon Province, 8 June 1960; USNM 120373, mature male, ca. 1,800 mm, Lake Nicaragua, off San Carlos, September 1943, L. Marden; MNHN A 9652, mounted skin of male, 1,860 mm [syntype of *Carcharias (Prionodon) leucas*], Antilles; USNM 16887, skin, skull, and jaws of mature male, 1,930 mm (holotype of *Eulamia nicaraguensis*), Lake Nicaragua, 1876, J. F. Bransford; USNM 105262, skin of mature male, ca. 2,250 mm, Virginia, Mundy Point, 23 September 1937, G. Turner; GVF 2353, mature male, 2,355 mm, Gulf of Thailand, Chumphon Province, 3 mi offshore E of Langsuan, ca. 9°59'N, 99°12'E, 3-6 August 1960; AMS IB.6007, jaws, clasper, and skin sample from mature male, 2,500 mm, Australia, Queensland, Gillett Cay, Swain Reefs, 15 October 1962; AMS IB.1225, teeth and skin sample from male, 2,544 mm [holotype of *Galeolamna (Bogimba) bogimba*], Queensland, Fraser Island, Bogimbah, 16 March 1943; AMS IB.6352, teeth and skin sample from female, ca. 2,700 mm, Australia, New South Wales, Sydney, Middle Harbour, 29 January 1963, E. Campbell; ORID 713, female, 2,770 mm, South Africa, Durban, 14 May 1963.

Also USNM 174073, head of small specimen, Australia, Northern Territory, East Alligator River at Cahill's Landing, 13 October 1948, R. R. Miller and W. H. Harney.

Also jaws at various institutions, including: UMMML 8462, Florida, Key Largo, 28 November 1958, S. Gruber and S. Kotzen; UCLA 62-56, three sets of jaws, Nicaragua, Rio San Juan, El Castillos Rapids, 31 March 1962, T. R. Howell and party; RNH 24697, New Guinea, Lake Jamoer, 24 March 1955.

Carcharhinus amboinensis (Müller and Henle, 1841)

Figure 42

Carcharias (Prionodon) amboinensis Müller and Henle, 1841:40-41, pl.19. Female, 29 in 9 lines (756 mm), Amboina.

Carcharias (Prionodon) henlei Bleeker, 1853:507-508. Male, 762 mm, Java, Batavia. [Preoccupied by *Carcharias (Prionodon) henlei* Valenciennes in Müller and Henle, 1841.]

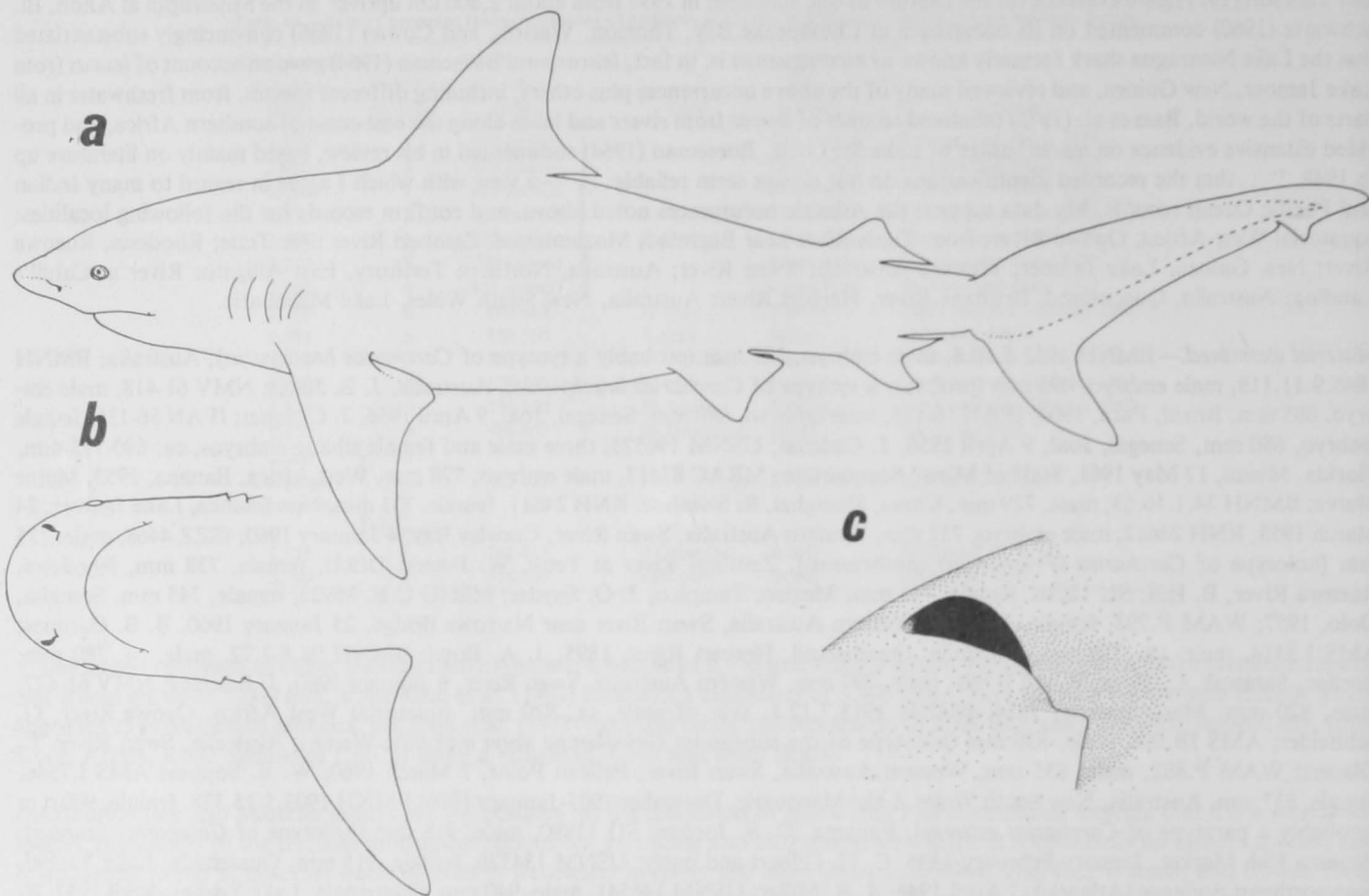


Figure 42.—*Carcharhinus amboinensis*, ORID 567, 1,460 mm TL, male from Durban: a, left side; b, underside of head; c, enlarged left nostril.

Carcharias (*Prionodon*) *brachyrhynchus* Bleeker, 1856:468. [Replacement name for *Carcharias* (*Prionodon*) *henlei* Bleeker, 1853.]

Diagnosis.—Large sharks, up to 2.23 m long, lacking an interdorsal ridge; tips of fins somewhat dusky, more so in juveniles than in adults; snout very short and bluntly rounded; internarial width 0.9-1.0 in preoral length; origin of first dorsal fin over or just posterior to pectoral axil; apex of first dorsal sharply rounded to pointed; origin of second dorsal in front of origin of anal fin; height of second dorsal 2.5-3.3% TL and 0.9-1.3 in length of its rear tip; dental formula usually $\frac{12-1-12}{11-1-11}$ but may be $\frac{11 \text{ to } 13-1-11 \text{ to } 13}{10 \text{ to } 12-1-10 \text{ to } 12}$; upper teeth broad, erect to slightly oblique, concave or shallowly notched laterally, with slightly coarser serrations basally; lower teeth erect, serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 89-95; caudal centra 96-102; total centra 185-195 (no data on the site of diplospondyly or the nature of the centra).

Common features which in combination distinguish *amboinensis* and *leucas* from all other *Carcharhinus* species are the lack of an interdorsal ridge, a very short, bluntly rounded snout, broad, virtually erect upper teeth, and no color pattern except for somewhat dusky fin tips. The best external character for separating *amboinensis* from *leucas* is the ratio of first dorsal height:second dorsal height (more than 3.1 in *amboinensis*, 3.1 or less in *leucas*). The number of teeth on each side of the lower jaw will, in most cases, also separate them (11 in *amboinensis*, 12 or sometimes 13 in *leucas*). The firmest criterion for identifying them is the number of precaudal vertebrae, *amboinensis* having 89-95 and *leucas* 101-123.

Nomenclatural discussion.—The validity of *amboinensis* was first brought to my attention by Jeannette D'Aubrey, Oceanographic Research Institute, Durban, who had noted that in her South African material seemingly of *leucas* there were some specimens with many fewer precaudal centra—93-95 versus a minimum of 110 in her *leucas* proper. Also, some of these specimens had only 11 teeth on each side of the lower jaw instead of 12 as usually found in *leucas*. Comparison with nominal species resembling *leucas* indicated that only two, *amboinensis* Müller and Henle (1841)⁹ and *brachyrhynchus* Bleeker (1856), had 11 teeth on each side of the lower jaw. Further investigation revealed that *amboinensis* and D'Aubrey's pseudo-*leucas* shared common attributes, and differed from *leucas*, in terms of the relative heights of the first and second dorsal fins. Accordingly D'Aubrey (1964) published a summarized account of her South African material in which she recognized *amboinensis* and distinguished it from *leucas* in having the vertical height of the first

⁹Müller and Henle (1841:40) described *amboinensis* as having $\frac{25}{25}$ teeth, but the holotype in the Leiden Museum has only 23 teeth across the lower jaw.

dorsal more than 3½ times that of the second dorsal (in *leucas* the first dorsal was less than 3½ times the height of the second). In this account also, she gave the dental formula of *amboinensis* as $\frac{12 \text{ or } 13-1-12 \text{ or } 13}{11 \text{ or } 12-1-11 \text{ or } 12}$ and of *leucas* as $\frac{12 \text{ or } 13-1-12 \text{ to } 14}{12 \text{ or } 13-1 \text{ or } 2-12 \text{ or } 13}$.

Subsequently Bass et al. (1973) reported in detail their findings (including the results from an unpublished thesis by D'Aubrey, 1971¹⁰) on a large sample of *amboinensis* (46 specimens) and *leucas* (at least 400 specimens) from South Africa. They concluded that "Vertebral counts provide a sure separation of these two species. Precaudal vertebrae number over 100, usually more than 110, in *C. leucas* and less than 100 in *C. amboinensis*." With respect to external characters they noted that "The ratio of the heights of the first and second dorsal fins is 3.2 or more in *C. amboinensis* and less than 3.2 in *C. leucas*." In their descriptions and supporting data they showed that differences in the dental formulae are not infallible for distinguishing the species even though the usual formula for *amboinensis* is $\frac{12-1-12}{11-1-11}$ and for *leucas* is $\frac{13-2-13}{12-2-12}$.

The above data from Bass et al. (1973) provide a firm basis for interpreting the world literature on species referable to *amboinensis* or *leucas*. However, the prime criterion of vertebral numbers has limited value for such a purpose, insofar as published descriptions only infrequently include such information. The second criterion (ratio of first to second dorsal fin heights) has much wider applicability, but even so there still remain some published descriptions, including those of nominal species, in which dorsal fin heights were not given. Various other possible criteria based on differences in proportional dimensions (e.g., prenarial length, preoral length, length from snout tip to upper caudal origin) were, therefore, sought in my data and those of Bass et al. (1973), but most of these proved to be too variable to be of much value. Despite this, two such criteria ($\frac{2\text{nd dorsal rear tip}}{2\text{nd dorsal height}}$ and length of upper lobe of caudal) are utilized

here (Table 39), along with the criteria of Bass et al., because they provide the only possibility of identifying some nominal species which were inadequately described and for which incomplete or no type material was preserved.

Perusal of Table 39 confirms the value of Bass et al.'s (1973) criteria for separating *amboinensis* and *leucas*, although the only absolute criterion is that of precaudal vertebral numbers (89-95 for *amboinensis*, 101-123 for *leucas*). With very few exceptions the ratio of first to second dorsal height (not less than about 3.1 or 3.2 for *amboinensis*, and 3.1 or less for *leucas*) will also distinguish the species.

There are too few data on *amboinensis* to evaluate the adequacy of the ratio $\frac{2\text{nd dorsal rear tip}}{2\text{nd dorsal height}}$, but without exception *leucas* has values of less than 1.00 while five of six specimens of *amboinensis* have values (1.03-1.27) greater than 1.00. The final two criteria used, length of upper caudal lobe and dental formula, are both very variable. Nevertheless, with respect to dental formula, the probability is high, as evidenced by the frequency distribution given here (Table 45), that a specimen with only 11 lower teeth on each side will be *amboinensis*. Upper caudal lengths show greater overlap in the two species, but, in general, *amboinensis* has a longer tail than *leucas*. To some extent, the diagnostic value of tail lengths is increased if cognizance is taken of growth change; in both species the tail, as a proportion of total length, becomes relatively shorter in specimens as they progress from half-grown to adult size.

Müller and Henle (1841:40) described *amboinensis* from a small specimen, probably recently born, from Amboina in the East Indies. The dimensions they gave for their specimen, when converted from inches and lines to millimeters, include a length from snout tip to caudal origin of about 550 mm, and a length of caudal (presumably upper caudal lobe) of 200 mm. These agree well with figures of 540 and 200 mm, respectively, made from the type—a mounted skin (RNH 2582) in the Leiden Museum—and kindly provided together with other information by M. Boeseman of that institution. The type strongly resembles *leucas*, and I had initially come to the conclusion after examining it that it was that species, but the data given here in Table 39 substantiate its referral to *amboinensis*. Müller and Henle, compared *amboinensis* only with *milberti* from which they found it differed in the form of the teeth and the pectoral fin.

Referral of *brachyrhynchus* Bleeker to *amboinensis* is based on an examination of the type and on additional data provided by M. Boeseman and shown in Table 39. The name *brachyrhynchus* was proposed by Bleeker (1856:468) as a replacement name for his earlier described *henlei* (1853:507) because *henlei* Bleeker was preoccupied by *henlei* Valenciennes in Müller and Henle, 1841. The type of *henlei* Bleeker, and hence of *brachyrhynchus*, is a small male specimen (RNH 7380) in the Leiden Museum. Its validity as the type might be questioned because of the difference between its actual total length, 710 mm, and its designated length of 762 mm as stated by Bleeker. Boeseman¹¹ has suggested that this apparent difference may have been due to an error of transcription, with Bleeker intending to list his type as 712 mm long rather than 762 mm. Support for this suggestion is provided by Dumeril's (1865) account of *brachyrhynchus* which was based on a personal communication from Bleeker and which states that the unique type was 1,714 mm long—there can be no question that this should read 714 mm, in which case the length is very close to 712 mm as suggested by Boeseman and the actual length of 710 mm as measured by Boeseman and myself.

Table 45.—Frequency distribution of number of teeth on each side of lower jaw in *Carcharhinus amboinensis* and *C. leucas*.

<i>Carcharhinus</i>	No. of teeth			No. of sharks
	11	12	13	
<i>amboinensis</i>	17	3		10
<i>leucas</i>	2	126	16	72

¹⁰D'Aubrey, J. D. 1971. The taxonomy of two shark species of the genus *Carcharhinus*. Unpubl. M.Sc. Thesis, 171 p. University of Natal, Durban, South Africa.

¹¹M. Boeseman, Curator of Fishes, Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Leiden, Netherlands, pers. commun. July 1969.

The only important feature in which the type of *brachyrhynchus* differs from other specimens of *amboinensis* studied here (see Table 39) is in the proportion $\frac{\text{1st dorsal height}}{\text{2nd dorsal height}}$ equalling 3.1 rather than 3.5-3.7. This is due at least in part to the type of *brachyrhynchus* having a lower first dorsal fin—9.2% of TL compared with 9.4% in the type of *amboinensis* and 11.1-12.0% in the two South African and one Western Australian specimens for which I give data here. The low height of the first dorsal fin in this specimen can be attributed to its state of development because, judging by the shape of the fin, in which the anterior margin is strongly convex and the apex reflexed posteriorly, the type was either a late embryo or very recently born, and as such its first dorsal fin had not completely “unfurled” or expanded and hence its height could be expected to be lower than in specimens which had had a longer free-living existence. No vertebral count is possible for this specimen because the vertebral column has been removed from the trunk region.

The apparently anomalous situation resulting from Bleeker describing *brachyrhynchus* (= *amboinensis*) while at the same time he recognized Müller and Henle's *amboinensis* as a separate species is a result of Bleeker's misidentification of *amboinensis* Müller and Henle. Bleeker's (1854) own description of *amboinensis*, together with his illustration of it labelled plate 5 in an unpublished Bleeker Atlas in the Leiden Museum, leave no doubt that his *amboinensis* is referable to *plumbeus*.

Of the few reports of *amboinensis* in the literature most are either compilations from Müller and Henle or from Bleeker, or else are listings only which cannot be confirmed. Three exceptions are those of D'Aubrey (1964) and Bass et al. (1973)—already referred to—and Krefft (1968) who reported and illustrated a small specimen from Nigeria (characters shown on Table 39). Krefft's specimen is unusual in having the length of the second dorsal rear tip less than the vertical height of the second dorsal (hence resembling *leucas*) but its other features agree with *amboinensis*. Reports under different specific names but seemingly referable to *amboinensis* are those of Whitley (1943), Smith (1952b), and Fourmanoir (1964). Whitley described, as *spenceri*, five specimens from eastern Australia; one of these (his specimen A) from New South Wales is definitely *leucas* but the other four (his specimens B to E) from Queensland agree with *amboinensis* in dental formulae and in upper caudal lengths (see Table 39). Fourmanoir's brief account, as *leucas*, of specimens from Madagascar with dental formulae of $\frac{12-1-12}{11-1-11}$ is probably also referable to *amboinensis*.

Description (see also Table 46).—Large sharks, probably growing to at least 2.3 m TL, and possibly more. Midline of back between dorsal fins smooth, lacking an interdorsal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles rather large, loose spaced in small specimens but fairly close-packed in larger, each with three strong longitudinal ridges and corresponding sharp-pointed and strong posterior marginal teeth in small specimens, but with five teeth and three or five ridges predominating in a specimen 1,460 mm long.

Snout very short and bluntly rounded in contour. Anterior margin of eye slightly forward of front of mouth. Nostrils strongly oblique, with broadly ovate apertures, the anterior margin of each with a low but definite lobe.

Dental formula $\frac{12-1-12}{11-1-11}$ in 6 of 10 specimens counted by me or from the literature; $\frac{12-1-12}{11 \text{ or } 12-1-11 \text{ or } 12}$ in 2; $\frac{13-1-13}{11-1-12}$ in 1, and $\frac{11-1-11}{11-1-11}$ in 1. Upper teeth broad, oblique except for first one or two series on each side of symphysis, their lateral margins concave to shallowly notched, their medial margins weakly to moderately convex, both margins serrated, the serrations of moderate size but slightly coarser basally; one small symphyseal tooth. Lower teeth narrower than upper, erect or nearly so, both margins concave basally but the medial margins weakly convex distally, serrated, the serrations somewhat finer than those of upper teeth; one small symphyseal tooth. The teeth were well illustrated in Smith (1952b, pl. 31) and in Bass et al. (1973, pl. 8).

First dorsal fin high and long based, falcate, its apex sharply rounded; origin of first dorsal over or just behind axil of pectoral fin. Second dorsal fin large and high, almost equal to anal fin; length of second dorsal rear tip 1.03-1.27 times second dorsal height in five specimens, but 0.92 in one; origin of second dorsal anterior to anal fin origin by a distance up to about two-fifths of anal base. Pectoral fin broad based, moderately long, slightly falcate; origin of pectorals below the third gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal does not reach to first dorsal axil in small specimens but reaches beyond axil to about two-fifths along first dorsal rear tip in a specimen 1,460 mm long.

Color of the 1,460 mm specimen before preservation was gray above, white below; the tips of the second dorsal fin and the lower caudal lobe were slightly dusky, as were also the upper anterior margin of the caudal, the distal half and trailing margin of the pectoral fin on the underside, and the underside of the pelvic fin.

Vertebral counts of two specimens are given in Table 46 and of another 18 specimens in Table 47.

The smallest specimen of *amboinensis* that I have seen was 710 mm long (type of *brachyrhynchus*) and its features, particularly the shape of the first dorsal fin, suggest that it was either a late embryo or recently born. Krefft (1968) reported a free-living specimen of 720 mm from Nigeria, and Bass et al. (1973) recorded another of 750 mm from South Africa in which the umbilical scar was not fully healed. If my identification of them as *amboinensis* is correct, the four specimens from Queensland, Australia, described by Whitley (1943) as *spenceri* were free living at lengths of 732 and 804 mm.

Bass et al. (1973) gave the size at maturity in the male as about 1,950 mm; their specimens up to 1,940 mm were immature, while one of 1,960 mm had fully developed claspers. The 1,275 mm male described (as *zambezensis*) from South Africa by Smith (1952b) was immature, while the 1,460 mm male, also from South Africa, that I have seen was similarly immature with a clasper length of only 1.9% TL. For females, the only firm information on size at maturity is from Bass et al. (1973) who noted that one of 2,230 mm was mature while another of 1,980 mm was probably close to maturity. There are no data on litter size unless it is accepted that Fourmanoir's (1964) material (as *leucas*) from Madagascar is *amboinensis*; if so, his report of a gravid female of 2,210 mm containing five 440 mm embryos is the only information available. The largest specimens definitely reported are a 1,960 mm male and a 2,230 mm female from South Africa (Bass et al. 1973).

Table 46.—*Carcharhinus amboinensis*, proportional dimensions in percentage of total length.

	♂ 900 mm Western Australia WAM P25037- 002	♂ 1,275 South Africa Algoa Bay	♂ 1,460 mm South Africa Durban ORID 567
Snout tip to			
outer nostrils	—	2.9	2.5
eye	6.3	—	5.8
mouth	6.8	7.0	5.7
1st gill opening	15.0	—	16.1
3d gill opening	—	—	19.1
5th gill opening	19.8	22.4	21.0
pectoral origin	17.6	20.8	19.6
pelvic origin	49.6	49.7	48.4
1st dorsal origin	31.3	27.0	26.3
2d dorsal origin	59.7	59.3	59.7
anal fin origin	—	60.5	61.3
upper caudal origin	76.1	71.0	71.6
lower caudal origin	—	—	71.1
Nostrils			
distance between inner corners	7.3	7.0	6.6
Mouth			
width	11.2	9.6	9.8
length	4.8	4.2	4.4
Labial furrow lengths			
upper	—	—	0.3
lower	—	—	0.5
Gill opening lengths			
1st	2.9	3.1	3.2
3d	3.2	3.6	3.3
5th	2.6	2.6	2.4
Eye			
horizontal diameter	1.6	1.4	1.3
1st dorsal fin			
length of base	11.9	11.3	13.1
length posterior margin	3.9	5.4	4.3
height	11.6	12.0	11.1
2d dorsal fin			
length of base	4.6	4.4	4.6
length posterior margin	3.7	3.4	3.8
height	2.9	3.3	3.0
Anal fin			
length of base	4.9	4.2	4.5
length posterior margin	2.8	3.4	3.4
height	2.7	3.8	3.6
Pectoral fin			
length of base	6.9	—	7.5
length anterior margin	20.0	22.2	20.0
length distal margin	—	—	17.2
greatest width	—	—	11.5
Pelvic fin			
length of base	—	5.6	6.4
length anterior margin	6.7	6.3	6.6
length distal margin	—	—	6.7
length of claspers	—	—	1.9
Caudal			
length of upper lobe	29.9	29.0	28.9
length of lower lobe	13.8	—	13.3
Trunk at pectoral origin			
width	—	—	13.8
height	—	—	12.9
Dental formula	11-1-11	12-1-12	12-1-12
Vertebrae	11-1-11	11-1-11	11-1-11
precaudal	90	—	94 ¹
caudal	—	—	96
total	—	—	190

¹Data from A. J. Bass, Western Australian Museum, Beaufort St., Perth, pers. commun. July 1976.

²Data from Smith (1952a) as *C. zambezensis*.

³Data on vertebral numbers from J. D. D'Aubrey, Assistant Research Officer, Oceanographic Research Institute, 2 West St., Durban, pers. commun. July 1963.

Table 47.—Vertebral numbers in 18 specimens of *Carcharhinus amboinensis*.

Specimens	Precaudal	Caudal	Total
Nigeria (Krefft 1968)	95	102	197
Gulf of Aden (D'Aubrey ³)	89	99	188
16 specimens, South Africa (Bass et al. 1973)	90-95 (mean 92.9)	—	185-195 (mean 190.5)
Range (including counts from Table 46)	89-95	96-102	185-195

³D'Aubrey, J. D. 1971. The taxonomy of two shark species of the genus *Carcharhinus*. Unpubl. M.Sc. Thesis, 171 p. Univ. Natal, Durban, South Africa.

Distribution (see also Material examined).—The dearth of specimens and confirmable reports of *amboinensis* is such that no firm picture of its distribution is so far available. The holotype was from the sea at Batavia, Java, and the holotype of the conspecific *brachyrhynchus* was from the adjacent Amboina, also in the East Indies. Whitley's (1943) specimens of *spenceri*, if truly *amboinensis*, were from Queensland, Australia. Bass¹² provided data on a specimen from Western Australia. The species is now well known from the Natal-coast of South Africa from Bass et al.'s (1973) admirable account, and is probably also at Madagascar judging by Fourmanoir's (1964) report (as *leucas*) of specimens with a dental formula of $\frac{12-1-12}{11-1-11}$. An earlier account (also as *leucas*) by Fourmanoir (1961) from Madagascar contains too little information to identify the species with certainty; the measurements given suggest that both *leucas* and *amboinensis* were involved. Bass et al. (1973) recorded *amboinensis* from the Gulf of Aden, and Krefft (1968) reported it from the eastern Atlantic, off Nigeria. The above localities all lie within the range of *leucas*. According to Bass et al. (1973), *amboinensis* is an in-shore species, but tends to live in deeper waters than *leucas*, and was not taken by them in fresh or brackish water. However, subsequently Bass (see footnote 12) provided data on a Western Australian specimen which had been taken in brackish water at the base of King's Cascade, Prince Regent River, Kimberley District. Also, three of the four Queensland specimens which Whitley (1943) described as *spenceri* were taken in the Fitzroy River or Fitzroy River estuary during March, at which time according to data in Kennedy (1975) the salinity is not more than 5‰ even at the mouth of the river.

Material examined.—RNH 7380, male, 710 mm [holotype of *Carcharias (Prionodon) brachynchos*], sea at Batavia; RNH 2582, mounted skin of female, 715 mm [holotype of *Carcharias (Prionodon) amboinensis*], Amboina, H. C. Maclot; AMS IB.1221, some teeth and a sample of skin from a female, 732 mm, Queensland, Fitzroy River, Mackenzie Island, 19 March 1943; ORID 567, male, 1,460 mm, South Africa, Durban, March 1963.

Carcharhinus melanopterus (Quoy and Gaimard, 1824)
Figures 43, 44

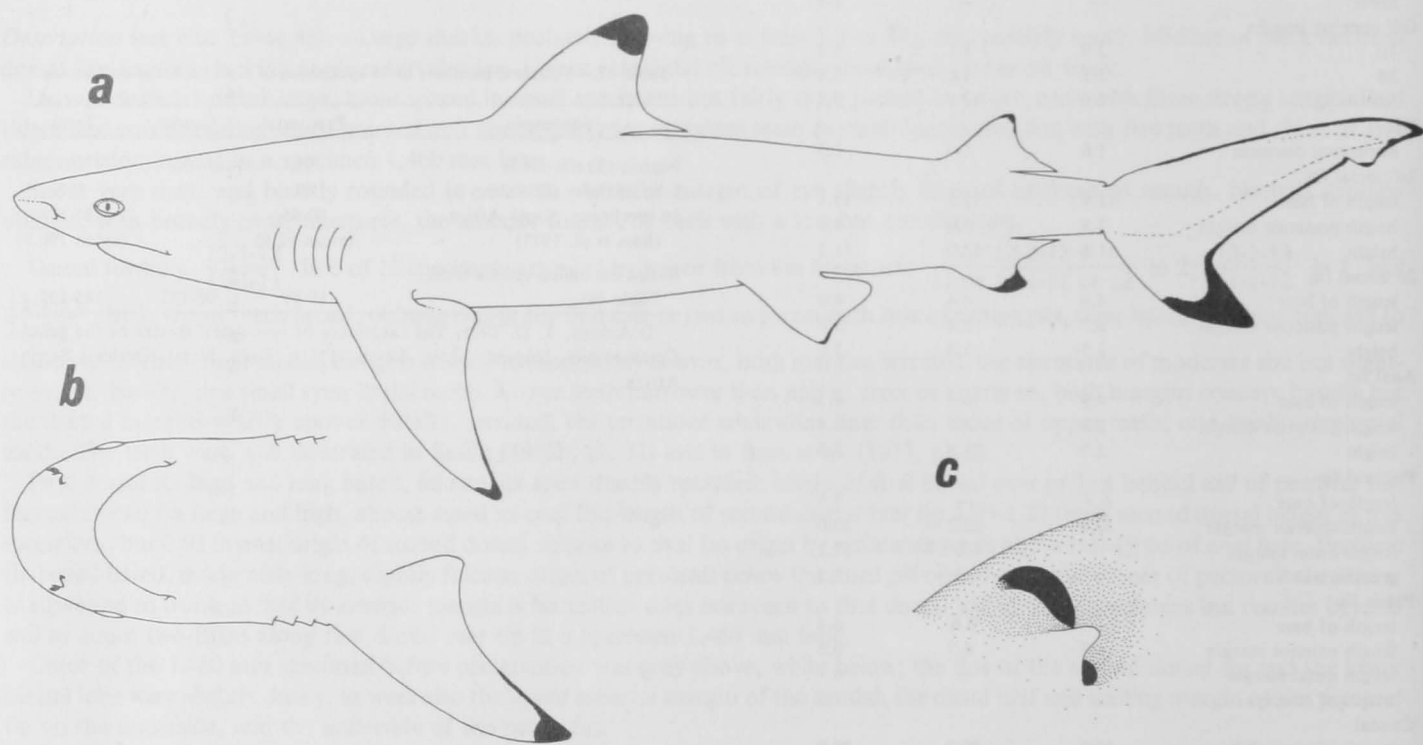


Figure 43.—*Carcharhinus melanopterus*, USNM 179126, 991 mm TL, female from Red Sea: a, left side (apex of anal fin reconstructed); b, underside of head; c, enlarged left nostril.

Carcharias melanopterus Quoy and Gaimard, 1824:194-196, pl. 43, figs. 1, 2. Holotype, male, ca. 590 mm, Vaigiou (Waigau) Island, New Guinea; paratypes, three males, two of them 513 and 529 mm from New Guinea, the third, ca. 530 mm, from Vanicoro Island, Santa Cruz Islands; species also observed at the Marianne Islands.

Carcharhinus commersonii Blainville in Vieillot, 1825:90. Based on an illustration of a shark in Lacepède (1798), which in turn was derived from a figure in a manuscript by Commerson.¹³ The illustration is of a male, 6 ft (1,829 mm) long, from the Indian Ocean.

¹²J. Bass, Western Australian Museum, Beaufort St., Perth, pers. commun. July 1976.

¹³I have not seen the manuscript but it and its author are discussed by Bertin (1939) and also by Boeseman (1960) who reproduced parts of it and noted that his copy came from the Muséum National d'Histoire Naturelle of Paris.

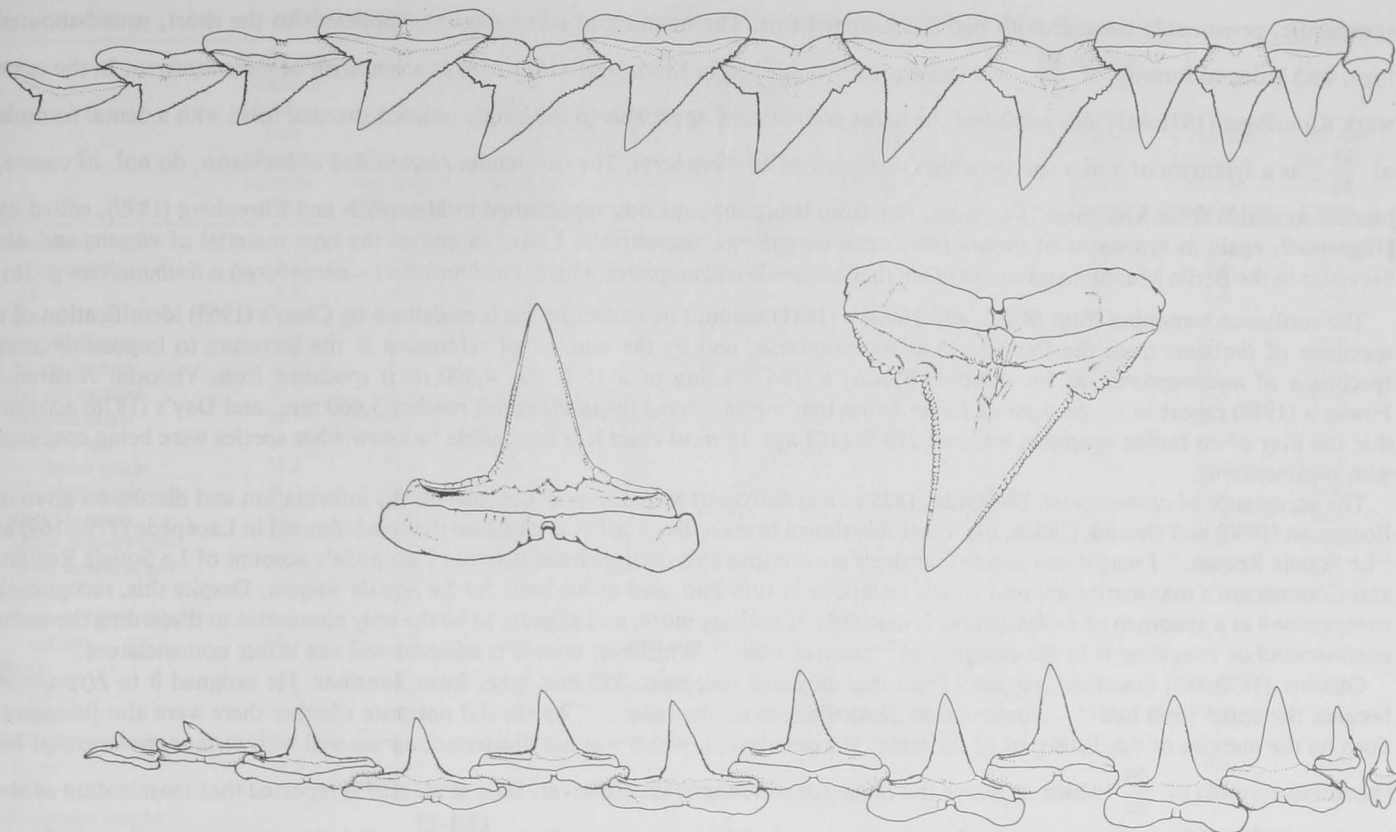


Figure 44.—*Carcharhinus melanopterus*, USNM 114630, ca. 1,000 mm TL, from the Solomon Islands: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

Carcharias (Hypoprion) playfairii Günther, 1870:362-363. Mounted specimen, 22 in (559 mm) long; Lieut.-Col. Playfair's collection, Zanzibar.

Carcharias marianensis Engelhardt, 1912:647. One female specimen, 400 mm; Marianas, Guam Island.

Diagnosis.—Moderate-sized sharks, up to 1.80 m long, lacking an interdorsal ridge; tips of first dorsal and lower lobe of caudal fin prominently black and, to a lesser extent, all of the other fins are similarly dark tipped or dark margined; snout short and bluntly rounded; internarial width 0.9-1.1 in preoral length; origin of first dorsal fin about over inner pectoral corner; apex of first dorsal sharply rounded to pointed; origin of second dorsal about over anal fin origin; height of second dorsal 3.1-4.3% TL and 0.8-1.2 in length of its rear tip; dental formula usually $\frac{12-2-12}{11-3-11}$ but may be $\frac{11}{10}$ to $\frac{13-1}{12-1}$ or $\frac{2-11}{3-10}$ to $\frac{13}{12}$; upper teeth moderately narrow, oblique, notched laterally, with noticeably coarser serrations basally; lower teeth erect, serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 111-122; caudal centra 80-92; total centra 193-214; diplospondyly begins from pelvic origin to pelvic axil; diplospondylous centra regular in length; penultimate monospondylous centrum 1.3-1.7 times wider than long.

The combination of a prominent dark blotch on the first dorsal fin apex, a smooth back, and a short, bluntly rounded snout distinguishes *melanopterus* from all other species of *Carcharhinus*. The species most likely to be confused with *melanopterus* is the Australian *cautus*, but that species has only a narrow dark edging on the leading margin of the first dorsal fin, and many fewer precaudal centra.

Nomenclatural discussion.—*Carcharias melanopterus* Quoy and Gaimard, 1824 was designated as type species of the genus *Carcharhinus* Blainville, 1816 by Ruling 2(c) in Opinion 723 of the International Commission on Zoological Nomenclature (1965:32). The involved nomenclatural background to this ruling is given in papers by Boeseman (1960), White et al. (1961), and Garrick (1962a, b).

The original account of *melanopterus*, based on material from New Guinea and the western Pacific, and including an excellent colored plate, very clearly delineates this distinctive species. The four type specimens in the Paris Museum are in excellent condition. It is surprising, then, that there has been confusion in some subsequent identifications of the species. This confusion was probably engendered by Müller and Henle's (1841) account, where, remarkably, these authors described some specimens of *melanopterus* as having moderately long, pointed snouts, and others as having the characteristic short, rounded snouts; likewise they gave dental formulae of $\frac{31}{31}$ as well as $\frac{25}{25}$. These two forms had earlier been given separate specific status (*elegans* and *abbreviatus*) in a manuscript by Hemprich and Ehrenberg¹⁴ based on Red Sea specimens which were later examined by Müller and Henle and regarded as

¹⁴I do not know if the original manuscript is still in existence. Klunzinger (1871:658, 661) referred to it simply as "Symb. phys." and "Symb. phys. inedit." The plates from it were subsequently published under the editorship of Hilgendorf in Hemprich and Ehrenberg (1899).

conspicuous, presumably because both had black-tipped fins. The manuscript name *elegans*, applicable to the short, round-snouted form with a dental formula of $\frac{25}{25}$, was subsequently published in Klunzinger (1871:658) as a synonym of *melanopterus*. In the same work Klunzinger (1871:661) also published the name *abbreviatus*, applicable to the longer pointed-snouted form with a dental formula of $\frac{31}{31}$, as a synonym of a new species which he described as *ehrenbergi*. The two names *elegans* and *abbreviatus*, do not, of course, become available from Klunzinger's account, nor from being subsequently republished in Hemprich and Ehrenberg (1899), edited by Hilgendorf, again as synonyms of *melanopterus* and *ehrenbergi*, respectively. I have examined the type material of *elegans* and *abbreviatus* in the Berlin Museum and can confirm that *elegans* is *melanopterus* whereas *abbreviatus* (= *ehrenbergi*) is *limbatus* (see p. 28).

The confusion stemming from Müller and Henle's (1841) account of *melanopterus* is evidenced by Chen's (1963) identification of a specimen of *limbatus* from the Pescadores as *melanopterus*, and by the number of references in the literature to impossibly large specimens of *melanopterus*, as for example McCoy's (1867) listing of a 15 ft (ca. 4,500 mm) specimen from Victoria, Australia. Fowler's (1959) report in his account of Fijian fishes that *melanopterus* (as *spallanzani*) reaches 3,660 mm, and Day's (1878) account that the liver of an Indian specimen weighed 270 lb (123 kg). In most cases it is impossible to know what species were being confused with *melanopterus*.

The acceptance of *commersonii* Blainville, 1825 as a synonym of *melanopterus* depends on the information and discussion given by Boeseman (1960) and Garrick (1962a, b), where it is shown that *commersonii* was based on the shark figured in Lacépède (1798:169) "Le Squalé Requin." I would emphasize that there are considerable discrepancies between Lacépède's account of Le Squalé Requin and Commerson's manuscript account which Lacépède in turn had used as his basis for Le Squalé Requin. Despite this, recognizing *commersonii* as a synonym of *melanopterus* is plausible, if nothing more, and appears to be the only alternative to discarding the name *commersonii* or relegating it to the category of "incertae sedis." Whichever course is adopted will not affect nomenclature.

Günther (1870:363) described *playfairii* from one mounted specimen, 559 mm long, from Zanzibar. He assigned it to *Hypoprion* because the upper teeth had "... some obtuse denticulations on the base..." but he did not state whether there were also fine serrations on the margins of the distal part of the teeth. His description, which was not illustrated, agrees well with *melanopterus* except for the dental formula of $\frac{29}{28}$ which is above the range for *melanopterus*. However, Bass et al. (1975) reported that examination of the holotype (British Museum, no number) showed that its dental formula was, in fact, $\frac{12-1-13}{12-1-12}$, and the specimen was "... similar to *Carcharhinus melanopterus* in all ascertainable respects." Accordingly I follow these authors in treating *playfairii* as a junior synonym of *melanopterus*.

Three lines of evidence support my decision to refer *marianensis* Engelhardt (1912:647) to the synonymy of *melanopterus*. Firstly, although Engelhardt's description which was based on one small specimen from Guam Island is meager and lacks an illustration, it shows that *marianensis* agrees with *melanopterus* in having a short, bluntly rounded snout, a black-tipped first dorsal fin, and in being light brown in color. Secondly, despite the type of *marianensis* being only 400 mm long it must have been either a late embryo or newly born because Engelhardt was able to discern that the teeth were oblique, serrated, and notched laterally; such teeth also occur in *melanopterus* which can be free living at lengths considerably less than 400 mm. Thirdly, not only does *melanopterus* occur at Guam but it is also the only one of the five species of *Carcharhinus* reported from there (Bryan 1973) which could fit the features of *marianensis*. I do not know if the type of *marianensis* still exists.

Whitley (1934:188) referred *melanopterus* to the earlier described *spallanzani* Peron and Lesueur in Lesueur, 1822, and this usage has been followed by Munro (1955) and Fowler (1959). This referral, as previously noted by Tortonese (1935-36) is quite unwarranted. Peron and Lesueur's published account of *spallanzani* from northwestern Australia is so brief (see p. 167 of this account) as to be not even identifiable to genus, and although the shark was said to have black tips on the pectoral fins, second dorsal fin, and lower lobe of caudal fin this does not identify it as *melanopterus*. Elucidation of the identity of *spallanzani* only became possible through study of unpublished manuscript material of Peron and Lesueur¹⁵ from the Le Havre Museum. This material clearly indicates that *spallanzani* is conspecific with *sorrah* (see p. 167).

Description (see also Table 48).—Small sharks, not exceeding 1.8 m TL. Midline of back between dorsal fins smooth, lacking an interdorsal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles close-packed, overlapping, subcircular in outline in small specimens, more nearly rhomboid in larger, each with three longitudinal ridges and corresponding posterior marginal teeth in small specimens, five or even seven in larger.

Snout short, bluntly rounded in contour. Anterior margin of eye above or just forward of front of mouth. Nostrils strongly oblique with broadly ovate apertures, the anterior margin of each with a moderately long, bluntly pointed lobe.

Dental formula $\frac{12-1 \text{ or } 2-12}{10 \text{ or } 11-2 \text{ or } 3-10 \text{ or } 11}$ in five of nine specimens counted; $\frac{13-2-13}{11 \text{ or } 12-1 \text{ to } 3-11 \text{ or } 12}$ in three; $\frac{12-2-12}{11-3-12}$ in one. Upper teeth moderately narrow, oblique except for the first two or three series on each side of symphysis, their lateral margins notched, their medial margins varying from almost straight to weakly concave or even slightly notched, both margins serrated, the serrations finer distally but coarser and irregular basally; one or two smaller symphyseal teeth. Lower teeth narrow, erect or only slightly oblique, both margins concave to notched basally, very finely serrated; one to three smaller symphyseal teeth. Bass et al. (1973) described and

¹⁵The manuscript includes descriptions and illustrations of fishes collected during Baudin's expedition to "Terres australes" on the corvettes *Geographe* and *Naturaliste* in 1800-4. I have seen only that part of it dealing with *spallanzani*.

Table 48.—*Carcharhinus melanopterus*, proportional dimensions in percentage of total length.

	♂ 427 mm			♀ 525 mm	♀ 616 mm			♂ 710 mm		
	Solomon		♂ 521 mm	Philippine	Australia			Marshall		
	Islands		Caroline	Islands	Northern	♂ 631 mm	♀ 642 mm	Islands	♀ 790 mm	♀ 991 mm
	New	♂ 513 mm	Islands	Leyte	Territory	Hawaiian	Gulf of	Rongelap	Hawaiian	Red Sea
	Georgia	New Guinea	Yap Island	USNM	USNM	Islands	Thailand	Atoll	Islands	USNM
	USNM	MNHN 1128	GVF 1934	151229	174072	USNM 52643	GVF 2320	USNM	USNM 51205	179126
	114631							140970		
Snout tip to										
outer nostrils	3.1	2.8	2.9	2.8	2.3	2.5	2.5	2.5	2.5	2.3
eye	6.8	6.2	6.1	5.9	5.7	5.4	5.7	6.0	5.8	5.6
mouth	7.3	6.2	6.5	6.1	6.0	6.0	5.8	6.3	5.8	5.6
1st gill opening	19.5	16.7	16.3	16.1	17.8	16.0	15.3	17.9	17.4	18.3
3d gill opening	21.3	19.6	18.7	18.5	20.3	17.7	18.2	20.0	19.7	21.1
5th gill opening	23.5	21.8	20.3	20.4	21.8	19.4	19.7	21.8	21.4	23.0
pectoral origin	22.3	20.7	19.6	19.6	21.2	18.5	19.0	20.7	20.5	22.3
pelvic origin	46.6	47.4	46.3	46.8	47.3	45.1	46.7	46.4	45.9	51.4
1st dorsal origin	33.8	31.8	31.0	30.3	31.6	29.8	30.3	30.8	29.6	33.3
2d dorsal origin	61.3	63.2	60.7	60.2	60.8	60.2	60.6	57.8	61.2	65.6
anal fin origin	62.3	62.6	61.2	59.8	60.2	59.8	59.6	59.3	60.6	66.1
upper caudal origin	74.0	75.5	73.5	73.2	73.9	72.6	73.8	74.3	73.1	78.2
lower caudal origin	73.2	74.6	72.8	72.5	73.6	71.9	72.9	73.8	72.5	77.4
Nostrils										
distance between inner										
corners	6.3	5.8	6.0	5.7	6.2	5.7	6.0	6.0	5.8	6.2
Mouth										
width	8.9	7.6	8.2	7.6	8.4	7.7	7.9	8.4	8.1	9.3
length	5.2	4.9	4.2	4.2	4.5	4.0	4.6	4.5	4.9	5.2
Labial furrow lengths										
upper	0.5	0.4	0.4	0.6	0.6	0.5	0.3	0.7	0.8	0.5
lower	0.5	0.7	0.4	0.5	0.5	0.5	0.4	0.5	0.6	0.8
Gill opening lengths										
1st	3.5	3.0	3.2	2.4	3.4	2.5	3.5	3.0	2.8	2.9
3d	—	3.3	3.5	2.6	3.6	3.0	4.2	3.4	3.2	3.6
5th	2.8	2.5	2.5	1.9	2.3	2.4	3.0	2.5	2.4	2.6
Eye										
horizontal diameter	3.0	2.5	2.5	2.4	2.4	2.2	2.3	2.4	2.2	2.0
1st dorsal fin										
length of base	8.9	9.3	8.9	9.7	8.9	8.2	9.5	9.4	9.4	10.3
length posterior margin	4.7	4.2	3.8	4.2	5.0	4.1	4.7	4.4	4.6	4.6
height	10.1	8.7	9.0	8.0	9.3	8.4	9.6	9.4	9.9	8.6
2d dorsal fin										
length of base	4.9	4.6	4.5	4.6	4.7	4.4	5.2	4.6	4.8	5.2
length posterior margin	3.9	4.2	3.3	3.8	4.4	3.3	3.8	3.9	3.8	3.5
height	3.7	3.7	3.7	3.4	3.6	3.5	3.9	3.9	4.1	4.0
Anal fin										
length of base	4.7	4.5	4.7	5.0	5.0	4.4	5.9	4.6	4.6	4.7
length posterior margin	3.5	4.0	3.4	3.6	3.7	3.5	3.8	3.4	3.8	3.7
height	3.8	4.1	3.8	3.8	4.2	3.8	4.4	3.8	4.1	3.7
Pectoral fin										
length of base	5.6	5.5	5.6	5.1	5.3	5.4	5.9	6.0	5.5	6.0
length anterior margin	18.8	18.6	17.5	17.6	18.1	17.2	18.8	17.1	19.3	19.0
length distal margin	14.8	12.7	13.1	13.9	14.5	13.0	14.6	13.4	14.5	15.1
greatest width	9.8	9.4	8.8	—	—	—	10.0	10.0	10.4	9.6
Pelvic fin										
length of base	5.9	5.6	5.0	4.8	5.1	4.6	5.1	5.2	5.1	5.8
length anterior margin	8.0	7.1	6.5	6.5	7.0	6.6	7.0	6.9	7.6	7.5
length distal margin	5.2	5.5	5.3	5.3	5.8	5.5	5.8	6.0	5.8	6.6
length of claspers	2.6	2.4	2.1	—	—	—	—	2.5	—	—
Caudal fin										
length of upper lobe	28.2	25.3	26.8	27.2	27.4	26.4	26.6	24.8	26.7	22.1
length of lower lobe	13.2	12.9	12.6	12.8	13.5	12.7	13.5	12.6	13.3	12.6
Trunk at pectoral origin										
width	12.7	11.7	11.2	11.4	13.0	11.9	10.4	12.4	12.8	13.4
height	10.1	11.7	9.6	11.5	10.3	10.1	—	11.6	10.8	11.6
Dental formula		13-2-13					12-2-12			
Vertebrae		12-1-12					10-3-10			
precaudal				117			116			
caudal				92			87			
total				209			203			

¹Paratype of *Carcharias melanopterus*.

illustrated slight sexual dimorphism in mature specimens, with mature males having the tips of the upper teeth somewhat more sharply curved than those of mature females.

First dorsal fin rather low, falcate, with a long rear tip; origin of first dorsal about over inner (posterior) corner of pectoral fin. Second dorsal fin high and long, equal to anal fin; length of second dorsal rear tip 0.8-1.2 (mean 1.0) times second dorsal height in 11 specimens; origin of second dorsal about over anal fin origin. Pectoral fins moderately long, falcate; origin of pectorals below levels of fourth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches almost quite to level of first dorsal axil.

Color after preservation in alcohol is light brown above, paler or cream colored below; a tongue of the paler color extends forward along each side from the pelvic base to the first dorsal origin, interrupting the otherwise uniformly brown flank; apical one-fourth to one-third of first dorsal fin black; second dorsal fin apex more or less black tipped; upper margin of dorsal caudal lobe dusky or black more so towards tip where posterior margin of terminal lobe is black edged; distal one-third to one-half of ventral caudal lobe black posterior (re-entrant) margin of caudal usually black edged; anal fin apex and anterior (outer) corner of pelvic fin more or less black tipped; pectoral fin with a black tip and usually with a black edging on the outer half or more of its distal margin.

Vertebral counts of two specimens are given in Table 48 and of another 26 specimens in Table 49.

Centrum diameter considerably greater than centrum length even in longest monospondylous centra at posterior of abdomen. Diplospondylous centrum length regular. Diplospondyly begins above anterior third to middle of pelvic base (but at posterior end of

base in one specimen). The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.60-0.75 (mean 0.68) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.14-1.25 (mean 1.18) in 9 specimens.

The largest embryo I have seen was 485 mm TL, while other specimens up to 625 mm had umbilical scars obvious or even still partly open, hence could have been embryos or newly born. However, Bonham (1960) reported two free-living specimens of 330 and 360 mm taken in the Marshall Islands in September and still showing umbilical scars. Similar observations are from Randall and Helfman (1973) for two free-living specimens—one of 370 mm from the Marshall Islands in December and the other of 490 mm (the latter with an umbilical scar) from Tahiti. Fourmanoir (1961) noted that size at birth in Madagascar material ranged from 460 to 520 mm. Juvenile and immature males examined by me ranged up to 915 mm TL, with clasper lengths of 2.1-2.8% TL; two mature males, 910 and 1,010 mm, had clasper lengths of 9.8 and 14.8% TL, respectively. Fourmanoir (1961) gave data on a mature male, from Madagascar, of 1,100 mm with a clasper length of 12.7%. Bass et al. (1973) noted that males from 1,090 to 1,160 mm were mature in their material from the southwest Indian Ocean. Melouk (1957) described eggs and sperm and the development of the embryo in material from the Red Sea. He observed that the number of eggs in each uterus was generally two, that in June pregnant females contained either very small embryos 30-40 mm long, or large embryos of 500 mm, and he suggested that development takes 16 mo. Gohar and Mazhar (1964), also reporting on Red Sea specimens, stated that pregnant females in December ranged from 1,200 to 1,310 mm long, that there were four embryos per litter, and that young were born either in January or in June. Fourmanoir (1961) gave comparable data for specimens from Madagascar where he found that there were two to four embryos per litter and young were born either in December-January or in June-July. He listed a female of 1,190 mm as containing three embryos, 450 mm long, in November. Randall and Helfman (1973) reported the following data on the reproductive state of six females from the central Pacific: one female of about 1,120 mm from

Table 49.—Vertebral numbers in 26 specimens of *Carcharhinus melanopterus*.

Specimens		Precaudal	Caudal	Total
GVF 2467	Gulf of Thailand	116	87	203
GVF 2467	Gulf of Thailand	117	87	204
GVF 2467	Gulf of Thailand	117	87	204
GVF 2467	Gulf of Thailand	117	88	205
GVF 2467	Gulf of Thailand	119	88	207
GVF 2467	Gulf of Thailand	120	87	207
USNM 151230	Philippine Islands	116	90	206
MNHN 1129 ¹	Vaigiou (Waigiu)			
	Island	114	85	199
GVF 839	Palau Islands	122	92	214
GVF 195	Caroline Islands	117	87	204
GVF 1934	Caroline Islands	118	88	206
USNM 167437	Gilbert Islands	115	88	203
	2 specimens, Western			
	Australia ²	113-114	80-81	193-195
USNM 147421	Red Sea	116	86	202
	9 specimens, S.W.			
	Indian Ocean,	111-117	—	197-204
	St. Brandon ³	(mean		
	2 specimens, S.W.	114.2)		(mean
	Indian Ocean,			199.7)
	Europa Island ³	119-120	—	203-208
Range (including counts from Table 48)		111-122	80-92	193-214

¹Holotype of *Carcharias melanopterus*.

²Counts from Whitley (1945).

³Counts from Bass et al. (1973).

Palmyra Island contained eggs in November. Of four others, about 1,240-1,400 mm, containing embryos, three were from the Line Islands and had four embryos each in October-November, and the size of the embryos ranged from about 74 to 295 mm, while the fourth female was from Eniwetok Atoll and contained only two embryos of about 116 and 118 mm in December. A sixth female of 1,150 mm, also from Eniwetok, had four embryos of 420-430 mm in June. Alcock (1890) noted that a female of 5 ft (about 1,500 mm) from the Bay of Bengal contained six embryos, each 1 ft (about 300 mm) long, but there is no way of checking whether his identification of *melanopterus* was correct. Bass et al. (1973) observed that females from their southwest Indian Ocean material were mature at 1,120-1,310 mm. Whitley (1967) reported that *melanopterus* (as *spallanzani*) from Australia were mature at 4 ft 3 in (about 1,300 mm) long.

Although the literature includes accounts that *melanopterus* reaches a very large size—up to 15 ft (ca. 4,500 mm) long—these cannot be substantiated and are out of keeping with the small size at which this species is known to be mature (minimum of 910 mm long for males, 1,120 mm for females). The largest specimen of either sex that I have seen was 1,155 mm long. Strasburg¹⁶ provided data on a central Pacific male of 1,343 mm. Herre (1936) reported that the largest specimen he saw at the Marquesas was 1,800 mm. This size, as a maximum, is in accord with Fourmanoir's (1961) data from Madagascar where he said that maximum length is 1,700 mm, though in a footnote to a table on page 64 of the same account he listed a male specimen 1,804 mm long.

Distribution (see also Material examined).—The abundance of *melanopterus* in the tropical-subtropical Pacific and Indian Oceans is evidenced by the relatively large number of specimens in museum collections, although undoubtedly the frequency with which *melanopterus* has been collected must also be due in part to its shallow, inshore habitat (often but not always associated with coral reefs) and to its colorful appearance which has attracted collectors. Data from the present study confirm its range from the central Pacific westwards through the Indian Ocean to the east African coast and the Red Sea, including numerous oceanic islands, the continental coast of Asia, and the northern half of Australia. Several accounts report it from the Mediterranean. Its supposed presence in the Atlantic cannot be corroborated. Its absence from the eastern Pacific is real, judging by the extensive collecting that has been done in that region but which has failed to include any specimens of *melanopterus*. This absence is surprising in view of the presence of *melanopterus* at widely separated oceanic islands in the central and western Pacific.

Based on specimens that I have examined the limits of its distribution are as follows: in the central Pacific to the east at the Hawaiian Islands in the north, and southwards through Palmyra, Christmas Island, and the Tuamotu Archipelago; in the western Pacific and Indian Ocean to the north at the Marshall Islands, Philippines, Gulf of Thailand, Andaman Islands, Maldives Islands, and the Red Sea, and to the south at the eastern, northern, and western coasts of Australia and at New Caledonia.

Of the numerous literature reports of *melanopterus*, many are mere listings and some are in error, but taking these into account they still give *melanopterus* much wider distributional limits than does my own material. They indicate with a fair degree of confidence that *melanopterus* is present at most of the tropical-subtropical islands of Oceania, except for the more easterly groups where it is either rare or possibly absent. Randall in Randall and Helfman (1973), for example, noted that although he frequently observed it in the Society Islands and the Tuamotus he "... rarely saw it in the Marquesas Islands. None were seen during a month of diving at the four islands of the Pitcairn Group. The species was present at Mangareva and Temoe of the Gambier Group, southern Tuamotus, but seems to be absent from Rapa and Îlots de Bass (Marotiri). None were seen at Raivavae, Tubuai, and Rurutu in the Austral Islands; however, only a few days were spent at each of these islands. Three other Pacific islands where blacktips were not observed... are Johnston, Marcus, and Easter." Literature reports also substantiate that *melanopterus* is abundant through the Indo-Australian region, extends to southern Japan and China in the north and westwards along both coasts of India to the Persian Gulf and the Red Sea, and southwards to Madagascar and adjacent islands and the east coast of Africa to at least southern Mozambique (lat. 22°S). Its distribution in the southwest Indian Ocean was reviewed by Bass et al. (1973) who discussed a long-standing but doubtful record of it from "Cape Seas." I am unable to confirm its presence at the Seychelles, although it could be expected to be there. Smith and Smith's (1963) listing from the Seychelles is not supported by their illustration which is of some other species, possibly *wheeleri*, while an earlier listing by Bradley (1940) seems to have been based only on a shark reported by the vernacular name "requin noir" in Hornell (1927) and Dupont (1935). It is perhaps significant that Wheeler (1953) did not record *melanopterus* in his account of the Mauritius-Seychelles Fisheries Survey; however, V. G. Springer¹⁷ informs me that he collected *melanopterus* at St. Brandon's (Cargados Carajos), which is on the Mascarene Plateau, during 1976, when the species was common.

Tortonese (1951a, b), on information received verbally from Professor Melouk of Fouad University of Cairo, reported *melanopterus* from the Egyptian coast of the Mediterranean where he regarded it as an immigrant from the Red Sea through the Suez Canal; likewise Gohar and Mazhar (1964) listed *melanopterus* as being present in the Mediterranean, but they did not state that they had actually seen specimens. Ben-Tuvia (1966) considered Tortonese's record to be doubtful because of possible confusion between *melanopterus* and other black-tipped species such as *limbatus* and *brevipinna*. More recently, Quignard and Capapé (1971a) identified *melanopterus* from off Tunisia and suggested it was a Red Sea immigrant, and Capapé (1975) listed it as common off Tunisia; doubtless these identifications are correct but there are no descriptive details accompanying them.

Several reports of *melanopterus* from the eastern Atlantic, including listings by Rochebrune (1882) from "Sénégalie" and by Poll (1949) from the Gulf of Guinea, have not been substantiated by subsequent studies in that area. Cadenat's extensive works on elasmobranchs from Sénégal and adjacent regions, published in numerous papers from 1937 onwards, do not include *melanopterus* in the fauna, while Poll (1951) later indicated that his (1949) account of *melanopterus* was referable to *limbatus*. There can be little or no doubt that all reports of *melanopterus* from the eastern Atlantic were similarly based on other species. The same must also be said of

¹⁶Donald W. Strasburg, Fishery Research Biologist, Bureau of Commercial Fisheries, Honolulu, Hawaii, pers. commun. November 1960, and made available data collected for his study of central Pacific sharks (Strasburg 1958).

¹⁷V. G. Springer, Curator, Division of Fishes, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, pers. commun. September 1979.

Miranda-Ribeiro's (1923, not seen) account of *melanopterus* from Brazil—which Bigelow and Schroeder (1948) interpreted as *leucas*—and of McCoy's (1867) record from Victoria, Australia.

Material examined.—RNH 15957, four embryos, 260-275 mm, Red Sea, Kameron, 9 January 1936, J. H. Ziesel; AMS IB.8285, female embryo, 325 mm, Australia, Queensland, Townsville, 1967, G. Coates; BMNH 70.6.14.22-3, two embryos, female, 328 mm, and male, 340 mm, Andaman Islands, F. Day; MSNG C.E. 34563, male embryo, 350 mm, Red Sea, Massaua; SOSC Ref. No. 200, male, 411 mm, Fakaofu Atoll, Taukalau Island, 27 February 1965; NMV 60-472, male, 425 mm, Red Sea, Raveyah, 1896, Steindachner; USNM 114631, male, 427 mm, Solomon Islands, New Georgia, Morovo Lagoon, May 1944, W. M. Chapman et al.; USNM 167437, female, ca. 440 mm, Gilbert Islands, Onotoa, 21 August 1951, J. E. Randall; USNM 140969, male, 445 mm, Marshall Islands, Rongerik Atoll, 20 July 1946, T. Kohler; GVF 2467, six males, 451-490 mm, Gulf of Thailand, Trat Province, about 2-3 mi offshore W and WSW of Goh Chang (ca. 11°56'N-12°03'N, 102°14'30"-102°17'45"E), 12 January 1961; NMV 61-434, two males, 451 and 910 mm, Red Sea, Hasani Island, 1895; MSNG C.E. 38305, female, 455 mm, New Guinea, Geelvink Bay, 1875, O. Beccari; AMS IB.8000, female, 455 mm, Australia, Northern Territory, Point Essington, Smith Point, 1967, D. Linder and S. Neary; USNM 140972, female embryo, 460 mm, Marshall Islands, Bikini Atoll, 18 July 1947, V. E. Brock et al.; BMNH 67.11.28.175, male, 476 mm, Bleeker; NMV 61-404, female, 480 mm, Batavia; USNM 140971, male, 480 mm, Marshall Islands, Bikini Atoll, 4 April 1946, L. P. Schultz et al.; USNM 140973, male, 482 mm, Marshall Islands, Bikini Atoll, 19 July 1947, V. E. Brock et al.; BMNH 1937.6.16.1, female embryo, 485 mm, Red Sea, Crossland; USNM 115285, female, 495 mm, Phoenix Islands, Hull Island Channel, 11 July 1939, L. P. Schultz; BMNH 46.2.16.116, female, 495 mm, Molucca Islands; ISZZ 4470, mounted skin of female, 495 mm, Red Sea, Hemprich and Ehrenberg; GVF 360, two females, 500 and 510 mm, south of Caroline Islands, Kapingamarangi, 15 July 1954; USNM 151229, two females, 500 and 525 mm, Philippine Islands, Leyte, Abuyog, 26 July 1909, *Albatross*; GVF 195, male, ca. 507 mm, Caroline Islands, Ifaluk Atoll; BMNH 74.11.19.27, male, 507 mm, Pelew Islands, Schmeltz; GVF 1934, female, 509 mm, and male, 523 mm, Caroline Islands, Yap Island, 9°24'30"N, 138°7'35"E, 5 January 1960; MSNG C.E. 38453, female, 510 mm, Philippine Islands, Leyte, Abuyog, *Albatross*; GVF 839, female, 511 mm, Palau Islands, 7 August 1956; MNHN 1128, male, 513 mm (paratype of *Carcharias melanopterus*), New Guinea, Quoy and Gaimard, *Uranie*; USNM 123883, female, ca. 515 mm, Guam, Tartugan Point, July 1945, M. H. Markley; BMNH 1951.1.16.2, female, 525 mm, and mature male, 935 mm, Red Sea, Sanafir Island, *Manihine*; MNHN 771, male, 529 mm (paratype of *Carcharias melanopterus*), New Guinea, Quoy and Gaimard, *Uranie*; MNHN 3463, mounted skin of male, ca. 530 mm (paratype of *Carcharias melanopterus*), Vanicoro Island, Quoy and Gaimard, *Astrolabe*; USNM 115287, female, 530 mm, Phoenix Islands, Hull Island channel, 10 July 1939, L. P. Schultz; USNM 114624, male, 532 mm, and female, 538 mm, New Caledonia, February 1944, W. M. Chapman; USNM 147421, male, 532 mm, Red Sea, Jiddah Fish Market, 10 July 1948; BMNH 90.11.17.9, female, 535 mm, Tongatabu, J. J. Lister; SOSC Ref. No. 200, female, 545 mm, Palmyra Island, 7 June 1964; RNH 4295, female, 550 mm, Amboina, S. Müller; NMV 61-422, male, 565 mm, Honolulu Fish Market, 1928, Pietschmann; GVF 101, male, ca. 568 mm, Tuamotu Archipelago, Raroia Atoll, Ohara Islet, 27 July 1952; USNM 151230, female, 570 mm, Philippine Islands, Cagayan de Jolo, 8 January 1909, *Albatross*; SMF 4594, male, 570 mm, Maldive Islands, Fadiffulu Atoll, 7 April 1958, L. Franzisket; AMS IB.2630, female, 570 mm, Northwest Australia; NMV 2932 and 2933 (old numbers), male, 575 mm, and female, 855 mm, Red Sea, January 1898; USNM 115286, male, 580 mm, Phoenix Islands, Canton Island lagoon, 24 May 1939, L. P. Schultz; NMV (—), male, 580 mm, Red Sea; USNM 166579, male, 585 mm, Marshall Islands, Arno Atoll, Ine Island, 27 August 1950, D. W. Strasburg et al.; NMV 2943 (old number), female, 585 mm, Red Sea, 1859; GVF 88, female, ca. 586 mm, Tuamotu Archipelago, Raroia Atoll; BMNH 58.4.21.510, male, 586 mm, Amboina; MNHN 1129, male, ca. 590 mm (holotype of *Carcharias melanopterus*) Vaigiou Island, Quoy and Gaimard, *Uranie*; SMF 2781, mounted skin of female, 595 mm, Red Sea, 1828, E. Rüppell; NMV 61-385, male, 600 mm, Red Sea, Djedda, 1895-96; SU 12767, male, 606 mm, Hawaiian Islands, Oahu, Honolulu, 1901; SU 14089, 607 mm, Hawaiian Islands, Oahu, Honolulu, 1889, O. P. Jenkins; BMNH 1908.7.13.22, male, 610 mm, Singapore, W. Morton; USNM 174072, female, 616 mm, Australia, Northern Territory reefs 1½-2½ mi W of Yirrkalla, northwest of Cape Arnhem, 25 August 1948, R. R. Miller et al.; NMV 61-362, male, 617 mm, Padang 1901, Schild; USNM 151540, male, 625 mm, Hawaiian Islands, Oahu, Honolulu, August 1924, E. K. Jordan; USNM 52643, male, 630 mm, Hawaiian Islands, 1901-02; GVF 2320, female, 642 mm, Gulf of Thailand, Surat Thani Province, near Goh Phangan, 18-22 July 1960; UZMK PO.687, female, 655 mm, Fiji, 1875, Wroblewsky; AMS IA.6567, male, ca. 660 mm, Australia, Queensland, Lindeman Island, G. P. Whitley; USNM 62483, male, ca. 670 mm, Hawaiian Islands, Oahu, Honolulu; USNM 140970, male, 710 mm, Marshall Islands, Rongelap Atoll, 16-28 June 1946, L. P. Schultz et al.; SMF 4593, female, 765 mm, Maldive Islands, Fadiffulu Atoll, 7 April 1958, L. Franzisket; USNM 51205, female, 790 mm, Hawaiian Islands, 1901; AMS IB.399, skin of male, ca. 790 mm, Australia, Northern Territory; NMV 50090 (old number), male, ca. 915 mm, Red Sea, 1880, Klunzinger; ISZZ 4473, mounted skin of female, ca. 950 mm, Red Sea, Hemprich and Ehrenberg; USNM 179126, female, 991 mm, Red Sea, 1962, E. Clark; USNM 114630, ca. 1,000 mm, Solomon Islands, south side of Kulambangra Island, Anchor Cove, 10 June 1944, W. M. Chapman; USNM 65783, male, ca. 1,010 mm, Tuamotu Archipelago, Takarava, 1899-1900, *Albatross*; ISZZ 7813, mounted skin of mature male, 1,055 mm, Red Sea, Hemprich and Ehrenberg; NMV (—), female, 1,060 mm, Second Red Sea Expedition; ISZZ 11916, mounted skin of female, ca. 1,150 mm, Taluit, Finsch; USNM 196036, jaws, skin sample, and measurements of male, 1,343 mm, equatorial Pacific, Christmas Island, 10 February 1955, Pacific Oceanic Fishery Investigations.

Carcharhinus cautus (Whitley, 1945)
Figures 45, 46, 47

Galeolamna greyi cauta Whitley, 1945:2-4, fig. 2. Female, 918 mm, Western Australia.

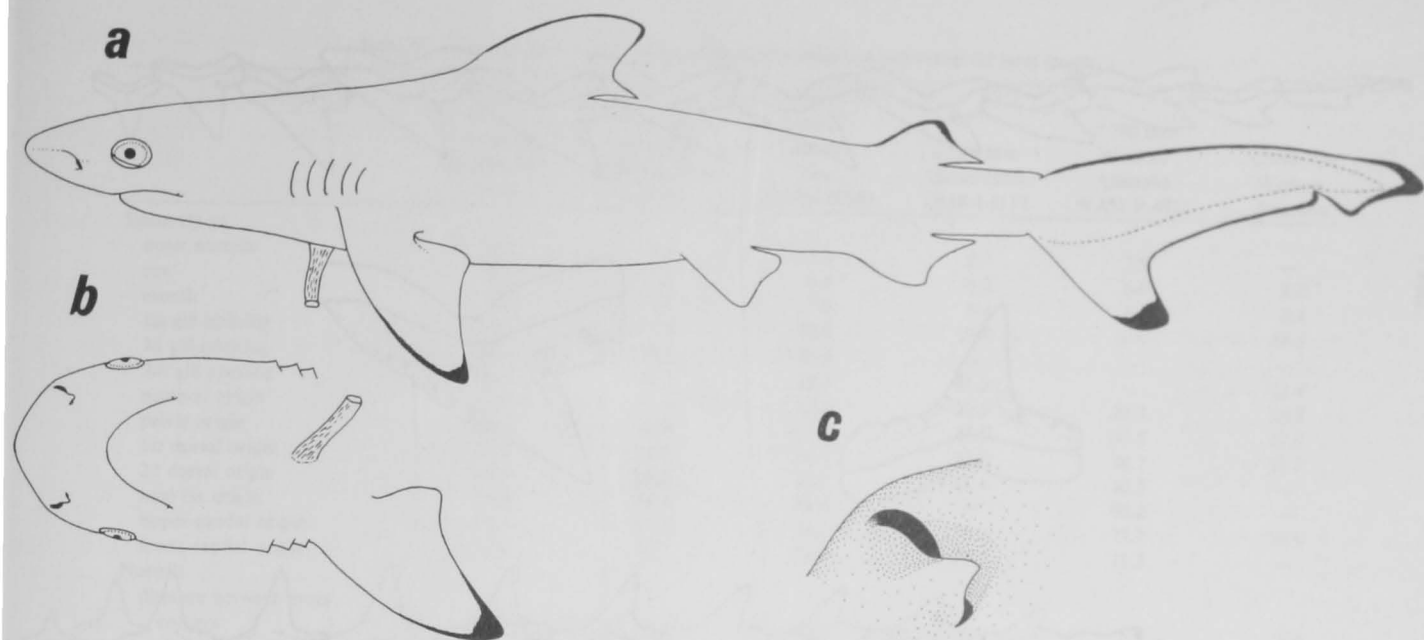


Figure 45.—*Carcharhinus cautus*, late embryo, BMNH 1927.10.28.2, 315 mm TL, female from Western Australia: a, left side; b, underside of head; c, enlarged left nostril.

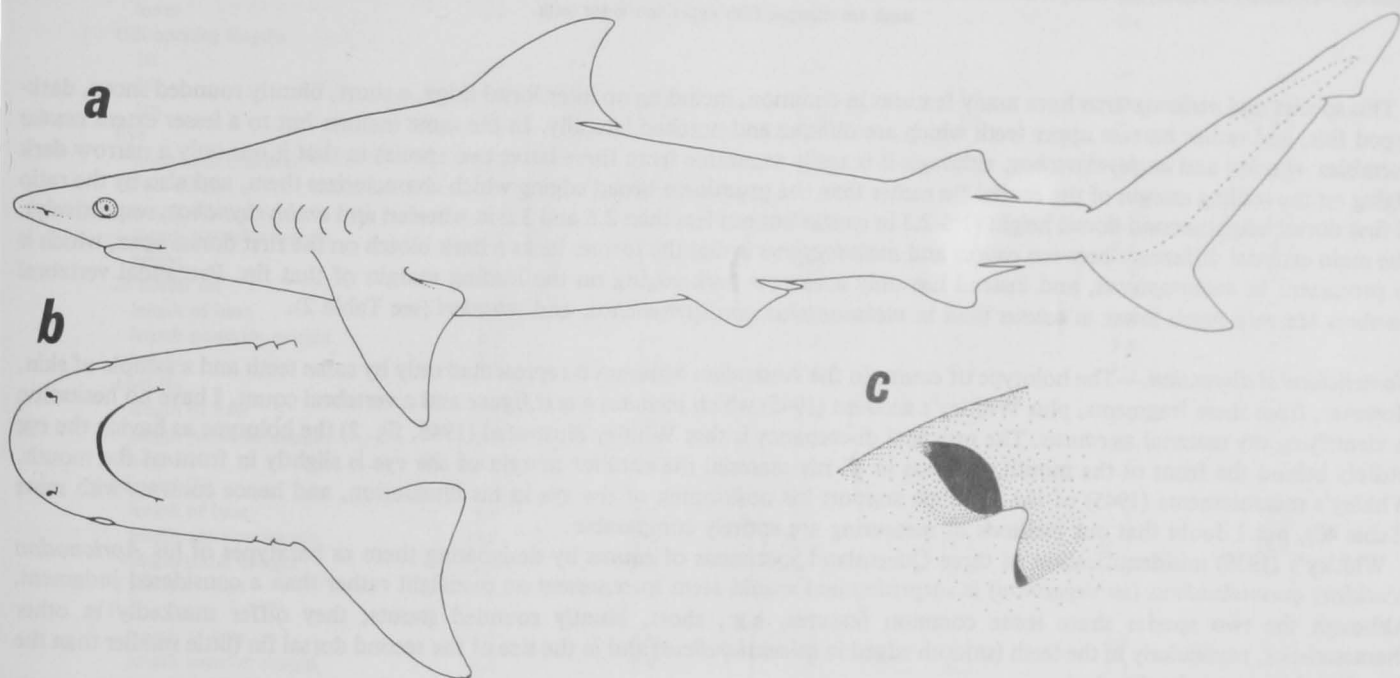


Figure 46.—*Carcharhinus cautus*, adult, WAM P.4911, 780 mm TL, male from Western Australia: a, left side; b, underside of head; c, enlarged left nostril. Note: Slightly modified from drawings made by A. J. Bass; color pattern not shown.

Diagnosis.—Moderate-sized sharks, up to 1.50 m long, lacking an interdorsal ridge; tips of pectorals and lower lobe of caudal fin dusky to black, while the leading margins of the pectorals, dorsals, and upper lobe of caudal are narrowly edged with dusky or black as is also the trailing margin of the whole caudal fin; snout short and bluntly pointed to rounded; internarial width 1.1-1.2 in preoral length; origin of first dorsal fin about over or slightly anterior to inner pectoral corner; apex of first dorsal sharply rounded to pointed; origin of second dorsal about over or slightly behind anal fin origin; height of second dorsal 3.1-4.1% TL and 1.0-1.1 in length of its rear tip; dental formula usually $\frac{12 \text{ or } 13-2-12 \text{ or } 13}{12 \text{ or } 13-1-12 \text{ or } 13}$ but may be $\frac{12 \text{ to } 14-1 \text{ or } 2-12 \text{ to } 14}{11 \text{ to } 13-1 \text{ or } 2-11 \text{ to } 13}$; upper teeth moderately narrow, oblique, deeply notched laterally, with markedly coarser serrations basally; lower teeth erect to oblique, concave to notched laterally, serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 86-90; caudal centra 70-81; total centra 160-171; diplospondyly begins at about the rear tips of the pelvic fins; diplospondylous centra regular in length; penultimate monospondylous centrum 1.0-1.3 times wider than long.

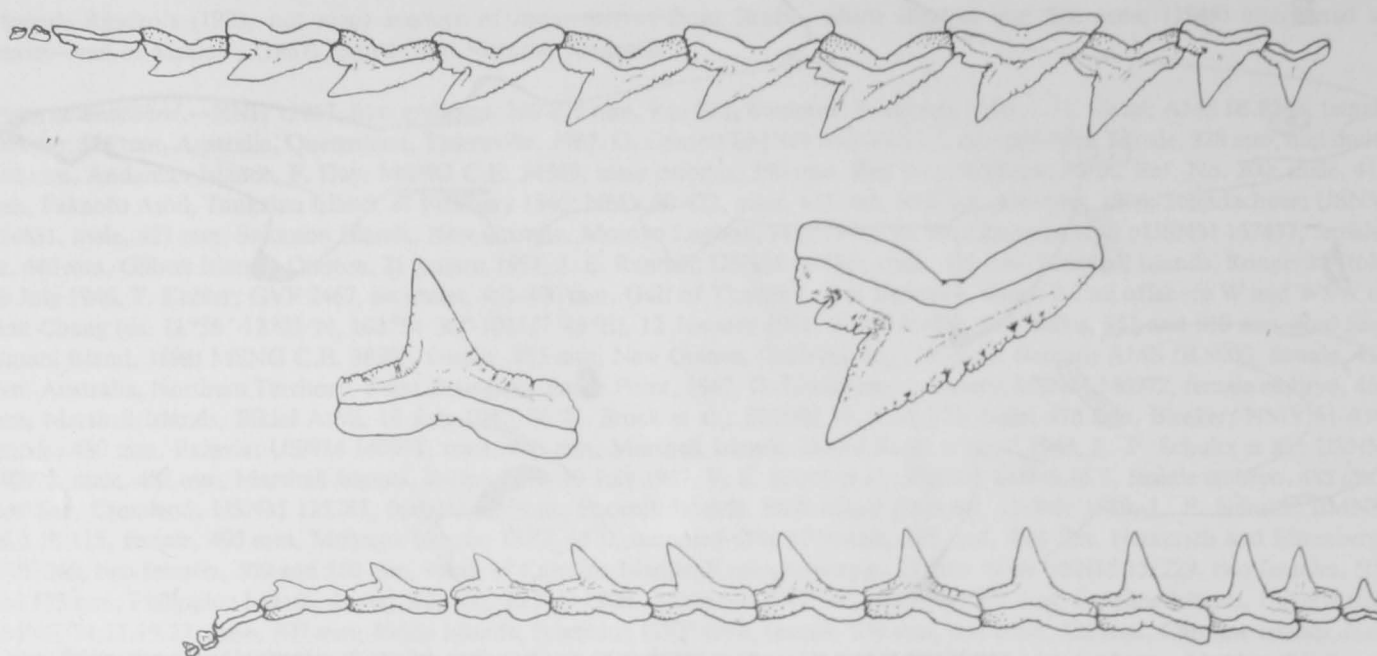


Figure 47.—*Carcharhinus cautus*, late embryo, BMNH 1927.10.28.2, 315 mm TL, female from Western Australia: right upper and lower teeth (symphysis to the right); ins teeth are enlarged fifth upper and lower teeth.

This species and *melanopterus* have many features in common, including no interdorsal ridge, a short, bluntly rounded snout, dark tipped fins, and rather narrow upper teeth which are oblique and notched laterally. In the same manner but to a lesser extent *cautus* resembles *wheeleri* and *amblyrhynchus*, although it is easily separable from these latter two species in that it has only a narrow dark edging on the trailing margin of the caudal fin rather than the prominent broad edging which characterizes them, and also by the ratio of first dorsal height:second dorsal height (1.9-2.3 in *cautus* but not less than 2.6 and 3.0 in *wheeleri* and *amblyrhynchus*, respectively). The main external difference between *cautus* and *melanopterus* is that the former lacks a dark blotch on the first dorsal apex, which is so prominent in *melanopterus*, and instead has only a narrow dark edging on the leading margin of that fin. Precaudal vertebral numbers are very much lower in *cautus* than in *melanopterus*, *amblyrhynchus*, and *wheeleri* (see Table 2).

Nomenclatural discussion.—The holotype of *cautus* in the Australian Museum is represented only by some teeth and a sample of skin. However, from these fragments, plus Whitley's account (1945) which includes a text figure and a vertebral count, I have no hesitation in identifying my material as *cautus*. The principal discrepancy is that Whitley illustrated (1945, fig. 2) the holotype as having the eye entirely behind the front of the mouth, whereas in all my material the anterior margin of the eye is slightly in front of the mouth. Whitley's measurements (1945) of the holotype support his positioning of the eye in his illustration, and hence contrast with mine (Table 40), but I doubt that our methods of measuring are entirely comparable.

Whitley's (1939) misidentification of three Queensland specimens of *cautus* by designating them as paratypes of his *Aprionodentus acutidens queenslandicus* (= *Negaprion*) is surprising and would seem to represent an oversight rather than a considered judgment. Although the two species share some common features, e.g., short, bluntly rounded snouts, they differ markedly in other characteristics, particularly in the teeth (smooth edged in *queenslandicus*) and in the size of the second dorsal fin (little smaller than the first dorsal in *queenslandicus*).

Description (see also Table 50).—Small sharks, not so far recorded as exceeding about 1.5 m TL. Midline of back between dorsal fins smooth, lacking an interdorsal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles close-packed, overlapping but with some small interspaces (especially in the embryos), subcircular in outline, slightly wider than long, with three longitudinal ridges and three posterior marginal teeth in the embryos and subadults, and five ridges and teeth in larger specimens.

Snout short, bluntly rounded except for the extreme tip which may be somewhat pointed. Anterior margin of eye is slightly forward of front of mouth. Nostrils strongly oblique, with broadly ovate apertures, the anterior margin of each with a long, pointed lobe.

Dental formula falling within the range $\frac{12 \text{ or } 13-2-12 \text{ to } 14}{11 \text{ to } 13-1 \text{ or } 2-11 \text{ to } 13}$ in five specimens counted. Whitley (1945) described the holotype as having $\frac{14-1-13}{12-1-13}$. Upper teeth somewhat narrow, oblique, their lateral margins deeply notched, their medial margins straight to sinuous, both margins irregularly serrated, the serrations largest basally, particularly on the lateral margins where there are several strong, irregular serrations; one or two symphyseal teeth which are only slightly smaller than those laterally adjacent to them. Lower teeth narrower than upper, erect near center of mouth, oblique towards side of mouth, their lateral margins notched, their medial margins concave to sinuous, their margins sparsely and irregularly serrated in small specimens, but more uniformly serrated in larger specimens; one or two small symphyseal teeth.

Table 50.—*Carcharhinus cautus*, proportional dimensions in percentage of total length.

	♂ 290 mm Western Australia BMNH 1927. 10.28	♀ 315 mm Western Australia BMNH 1927. 10.28	♀ 388 mm Australia Northern Terr. USNM 28690	♀ 585 mm Queensland QMB 1.6117	♂ 780 mm Western Australia WAM P.4911	1♀ 918 mm Western Australia
Snout tip to						
outer nostrils	2.6	2.5	3.2	2.7	2.9	—
eye	6.0	6.2	6.4	6.0	6.0	8.0
mouth	6.7	6.7	7.0	6.4	6.3	6.4
1st gill opening	17.7	18.4	18.0	17.8	—	18.4
3d gill opening	20.1	20.9	20.6	—	—	—
5th gill opening	22.2	23.2	22.4	21.3	—	22.4
pectoral origin	21.2	21.6	21.1	20.3	21.2	22.8
pelvic origin	46.2	47.0	47.7	47.6	45.5	47.9
1st dorsal origin	30.7	30.5	30.4	31.2	28.7	31.9
2d dorsal origin	60.6	60.0	60.7	61.4	60.3	—
anal fin origin	59.3	58.4	61.6	—	60.2	—
upper caudal origin	73.1	73.4	74.1	74.6	73.7	74.0
lower caudal origin	72.4	71.7	73.3	73.5	73.2	—
Nostrils						
distance between inner corners	6.4	6.2	5.8	6.0	5.9	5.6
Mouth						
width	7.9	7.6	7.7	8.5	8.1	8.5
length	4.3	4.4	4.4	4.6	4.7	—
Labial furrow lengths						
upper	0.3	0.5	0.5	—	0.3	—
lower	0.3	0.5	0.4	—	0.4	—
Gill opening lengths						
1st	2.9	2.5	1.9	2.7	—	2.8
3d	2.9	2.9	2.1	3.4	—	—
5th	2.1	1.9	1.5	2.4	—	1.9
Eye						
horizontal diameter	3.3	2.9	2.3	2.1	2.1	1.9
1st dorsal fin						
length of base	9.1	9.2	10.3	10.1	10.5	9.6
length posterior margin	3.8	3.6	4.1	4.3	4.1	4.7
height	6.5	6.3	7.7	9.2	7.9	—
2d dorsal fin						
length of base	4.0	4.9	5.5	4.9	5.4	4.8
length posterior margin	3.3	3.2	3.5	3.6	3.5	4.1
height	3.1	3.2	3.3	4.1	3.7	—
Anal fin						
length of base	5.7	5.7	4.9	5.5	5.9	5.1
length posterior margin	3.4	3.2	3.9	3.4	3.3	3.8
height	3.2	3.5	3.3	4.0	3.6	—
Pectoral fin						
length of base	5.5	5.7	5.9	6.0	6.7	5.7
length anterior margin	15.0	15.2	16.0	16.2	16.7	16.9
length distal margin	9.6	10.0	9.5	13.0	12.0	—
greatest width	8.1	9.2	—	—	9.4	—
Pelvic fin						
length of base	5.2	4.9	5.2	5.1	6.8	5.5
length anterior margin	6.7	5.9	7.0	6.7	7.1	7.0
length distal margin	4.8	5.1	4.9	5.8	5.4	—
length of claspers	2.2	—	—	—	4.2	—
Caudal fin						
length of upper lobe	26.2	26.7	26.3	26.7	26.7	25.6
length of lower lobe	11.9	11.7	12.9	12.1	12.3	12.7
Trunk at pectoral origin						
width	11.4	11.4	12.1	12.1	12.6	—
height	10.3	11.4	11.3	11.8	11.8	—
Dental formula	13-2-14 13-1-13	13-2-12 13-1-13	13-2-12 12-1-12	12-2-12 12-1-12	13-2-13 11-2-11	14-1-13 12-1-13
Vertebrae						
precaudal	90	86	88	90	90	90
caudal	78 +	81 +	79	81	80	70
total	168 +	167 +	167	171	170	160

¹Measurements of the holotype of the subspecies *Galeolamna greyi cauta* from Whitley (1945:2).

First dorsal fin rather low, falcate, its apex sharply rounded; origin of first dorsal is just anterior to, or over, level of inner (posterior) corner of pectoral fin. Second dorsal fin moderately large, almost equal to anal fin; length of second dorsal rear tip 0.9-1.1 times its height; origin of second dorsal about over or more often slightly behind anal origin. Pectoral fin short, broad basally but pointed distally; origin of pectoral fin about below the fourth gill opening; outer corner of pectoral fin when latter is adpressed to trunk so that its anterior margin is horizontal reaches at least two-thirds and more often four-fifths of distance along base of first dorsal.

Color after preservation is gray or brownish above, paler to white below; anterior margins of first and second dorsal fins and pectoral fin with narrow dusky to black edgings; anterior margin of upper lobe of caudal fin, and posterior margin of entire caudal fin similarly dusky to black edged; extreme tip of pectoral fin and tip of lower lobe of caudal fin dusky to black.

Vertebral counts of six specimens are given in Table 50 and of another four specimens in Table 51.

Centrum diameter usually greater than centrum length except for longest monospondylous centra which are almost or quite as long as wide. Diplospondylous centra regular. Diplospondyly begins behind the pelvic base, at about the level of the posterior tips of the

pelvic fins. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.78-1.00 (mean 0.95) and the

$\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.40-1.80 (mean 1.55) in five specimens.

The smallest, definitely free-living specimen I have seen was 585 mm TL, though it is likely that young are born at a much smaller size than this as another specimen of 388 mm had its yolk scar not fully closed but could well have been free living. The largest of seven embryos seen by me was 352 mm TL. Of the few male specimens available, one of 780 mm was clearly immature, with a clasper length equal to 4.2% TL. The female holotype, 918 mm, was reported by Whitley (1945) as immature. In the same account, Whitley noted that "This shark breeds at less than four feet [ca. 1,200 mm] in length, embryos being about a foot long. . . ." The mother of one of the embryos examined here was listed as 5 ft long (ca. 1,500 mm), and hence is the largest specimen recorded.

Distribution (see also Material examined).—The few specimens of *cautus* so far known are all from Australia and the Solomon Islands—a distribution which suggests that the species is likely to be much more widespread throughout the Indo-Australian region. Known localities so far include Western Australia from Shark Bay and northwards at about lat. 23°S; the east coast of Queensland from Moreton Bay northwards to Townsville; the west coast of Queensland, in the Gulf of Carpentaria at Karumba; Northern Territory at Darwin; and Ugi Island, Solomon Islands.

Table 51.—Vertebral numbers in four specimens of *Carcharhinus cautus*.

Specimens	Precaudal	Caudal	Total
WAM P.2857 Western Australia: Shark Bay	88	70 +	158 +
AMS IA.7767 Australia, Darwin	87	79	166
Western Australia ¹	86	77	163
Western Australia ¹	90	70	160
Range (including counts from Table 50)	86-90	70-81 +	158 + -171

¹Counts from Whitley (1967).

Material examined.—WAM P.2857, female embryo, 255 mm, Western Australia, Shark Bay, Dirk Hartog Island, 26 August 1944, G. P. Whitley; BMNH 1927.10.28.1-2, male embryo, 290 mm, and female embryo, 315 mm, Western Australia, 615 mi north of Fremantle; AMS IB.3159/2929, female embryo, 338 mm, Australia, Queensland, Karumba; AMS I.1623, two embryos, female, 340 mm, and male, 352 mm, Ugi Island, Solomon Islands, December 1887, A. Moreton; AMS I.1621, female embryo, 350 mm, Ugi Island, Solomon Islands, December 1887, A. Moreton; USNM 28690, female, 388 mm, Australia, Northern Territory, Port Darwin; QMB I.6117 female, 585 mm (paratype of the subspecies *Aprionodon acutidens queenslandicus*), Australia, Queensland, Cape Cleveland, January 1938, G. Coates; QMB 5577, female, not measured, (paratype of the subspecies *Aprionodon acutidens queenslandicus*), Australia, Queensland, Moreton Bay, H. A. Longman; QMB I.5976, male, ca. 720 mm (paratype of the subspecies *Aprionodon acutidens queenslandicus*), Australia, Queensland, Townsville, July 1937, G. Coates; WAM P.4911, male, 780 mm, Western Australia, Shark Bay, September 1960, F. Barrett-Lennard; AMS IB.1622, several teeth and a skin sample from female, 918 mm (holotype of the subspecies *Galeolamna greyi cauta*), Western Australia, Shark Bay, Herald Bight, 5 August 1943; AMS IA.7767, female, ca. 1,050 mm, Australia, Northern Territory, Darwin, M. Ward.

Carcharhinus amblyrhynchos (Bleeker, 1856)

Figures 48, 49

Carcharias (*Prionodon*) *amblyrhynchos* Bleeker, 1856:467-468. Female, 1,540 mm, Java Sea near Solombo Is.

Carcharias nesiotes Snyder, 1904:514-515, pl. 1, fig. 2. Holotype, female, 1,480 mm, Hawaiian Is., French Frigate Shoals; paratype, smaller female, Hawaiian Is., Laysan Is.

Galeolamna fowleri Whitley, 1944 (in part):255-256, fig. 2a. Holotype, male, about 5½ ft (1,676 mm) long, Western Australia, Exmouth Gulf.

Galeolamna tufiensis Whitley, 1949:24. Holotype, female, 1,481 mm, Papua, off Tufi Harbor; paratypes, female, 695 mm, and three males, 673, 738, and 2,545 mm, Papua, Tufi and Port Moresby.

Galeolamna coongoola Whitley, 1964:154-156, text fig. 1. Holotype, female, 940 mm, Australia, Queensland, Swain Reefs, Gille Cay; paratype, male, 1,448 mm, same locality as holotype except that it was taken at Capre Cay.

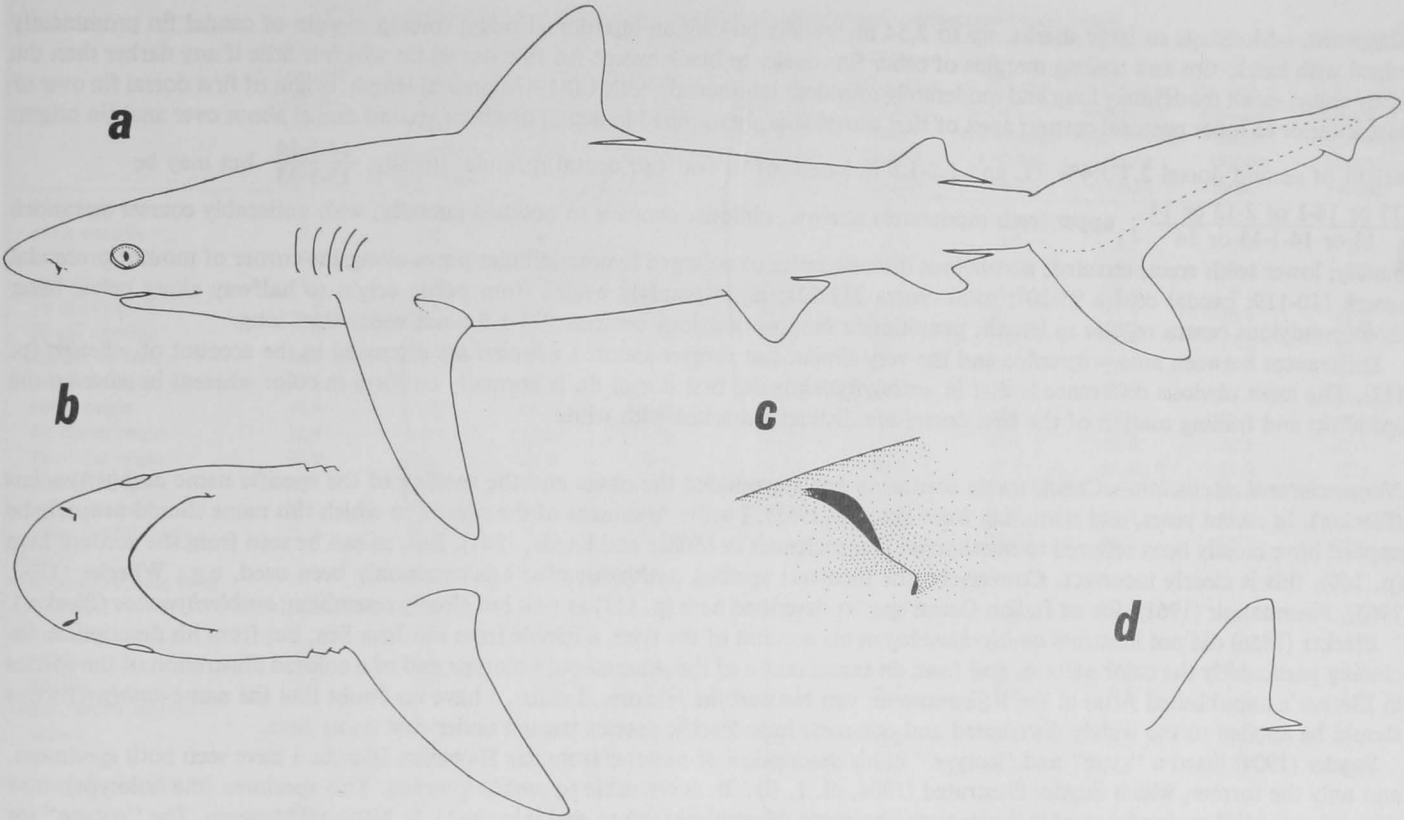


Figure 48.—*Carcharhinus amblyrhynchos*, USNM 140967, 853 mm TL, female from Marshall Islands: *a*, left side; *b*, underside of head; *c*, enlarged left nostril; *d*, first dorsal fin of USNM 140968, 600 mm TL, male from Marshall Islands.

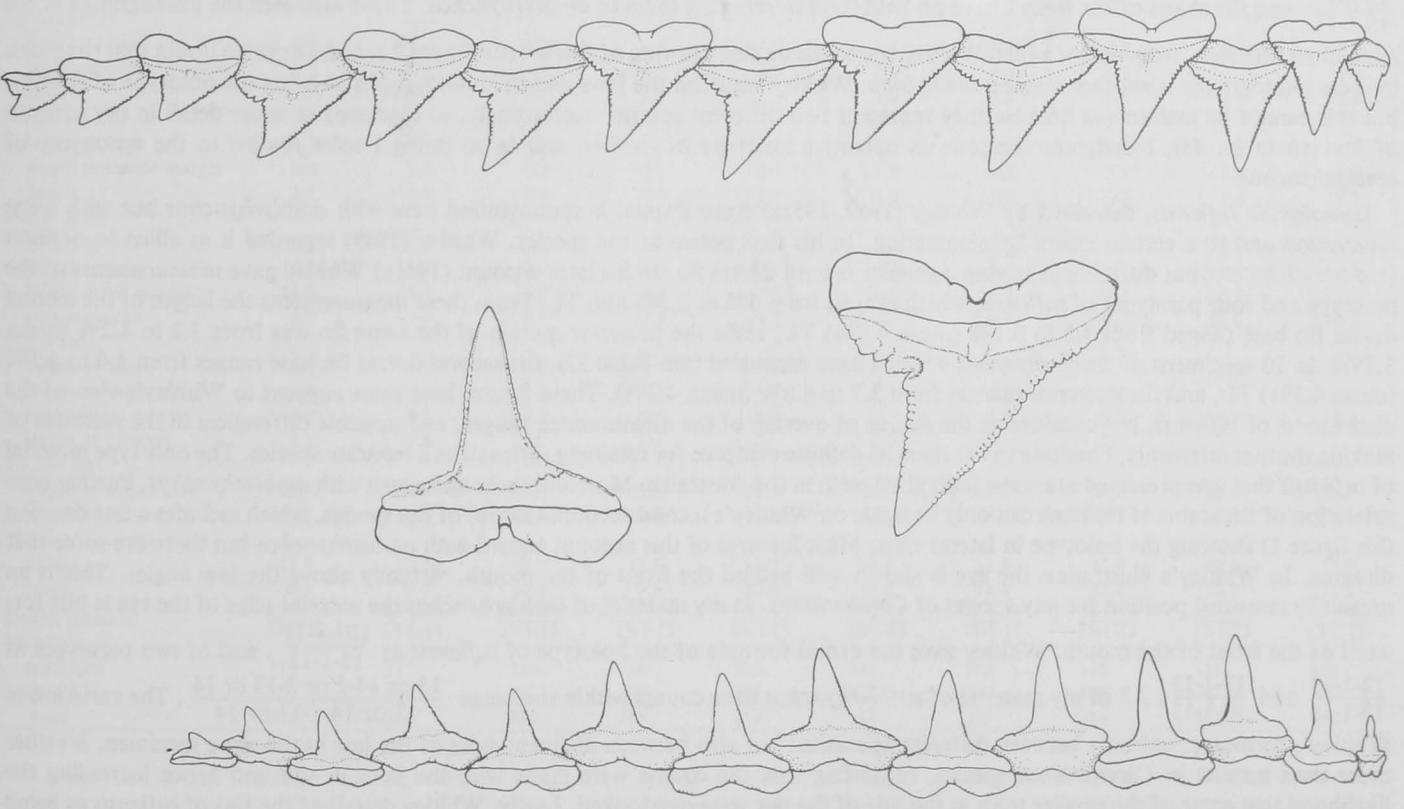


Figure 49.—*Carcharhinus amblyrhynchos*, USNM 140967, 853 mm TL, female from Marshall Islands: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

Diagnosis.—Moderate to large sharks, up to 2.54 m, usually lacking an interdorsal ridge; trailing margin of caudal fin prominently edged with black; tips and trailing margins of other fins dusky to black except for first dorsal fin which is little if any darker than the body color; snout moderately long and moderately rounded; internarial width 1.0-1.4 in preoral length; origin of first dorsal fin over or just anterior to inner pectoral corner; apex of first dorsal sharply rounded to acute; origin of second dorsal about over anal fin origin; height of second dorsal 2.7-3.4% TL and 1.2-1.6 in length of its rear tip; dental formula usually $\frac{14-1-14}{13-1-13}$ but may be

$\frac{13 \text{ or } 14-1 \text{ or } 2-13 \text{ or } 14}{13 \text{ or } 14-1-13 \text{ or } 14}$; upper teeth moderately narrow, oblique, concave to notched laterally, with noticeably coarser serrations

basally; lower teeth erect, serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 110-119; caudal centra 95-107; total centra 211-221; diplospondyly begins from pelvic origin to halfway along pelvic base; diplospondylous centra regular in length; penultimate monospondylous centrum 1.5-1.8 times wider than long.

Differences between *amblyrhynchos* and the very similar but shorter snouted *wheeleri* are discussed in the account of *wheeleri* (p. 113). The most obvious difference is that in *amblyrhynchos* the first dorsal fin is normally uniform in color whereas in *wheeleri* the apical tip and trailing margin of the first dorsal are distinctly marked with white.

Nomenclatural discussion.—Considerable confusion has surrounded the usage and the spelling of the specific name *amblyrhynchos* (Bleeker). In recent years, and stemming from Schultz (1953), Pacific specimens of the species to which this name should properly be applied have mostly been referred to *menisorrah* (Valenciennes in Müller and Henle, 1841). But, as can be seen from the account here (p. 160), this is clearly incorrect. Conversely, the incorrect spelling *amblyrhynchus* has commonly been used, e.g., Wheeler (1960, 1963), Fourmanoir (1961), for an Indian Ocean species described here (p. 111) as new but closely resembling *amblyrhynchos* (Bleeker).

Bleeker (1856) did not illustrate *amblyrhynchos* in his account of the type, a female from the Java Sea, but from his description, including particularly the color pattern, and from an examination of the skinned-out holotype and of a colored illustration of the species in Bleeker's unpublished Atlas at the Rijksmuseum van Natuurlijke Historie, Leiden, I have no doubt that the name *amblyrhynchos* should be applied to the widely distributed and common Indo-Pacific species treated under that name here.

Snyder (1904) listed a "type" and "cotype" in his description of *nesiotes* from the Hawaiian Islands. I have seen both specimens, and only the former, which Snyder illustrated (1904, pl. 1, fig. 2), is referable to *amblyrhynchos*. This specimen (the holotype), now skinned out, is a female comparable in size to the holotype of *amblyrhynchos*, and is in the U. S. National Museum. The "cotype" (or paratype) formerly at Stanford University (SU 12790) but now at the California Academy of Sciences, is clearly *galapagensis*. Böhlke (1953) listed a second paratype of *nesiotes* in his catalogue of type material at Stanford University but this specimen (SU 32027), represented only by a pair of jaws, also appears to be *galapagensis*.

Whitley (1944) described *fowleri* from Western Australia on the basis of photographs and a pair of jaws, in total representing either two or three specimens. I have examined the jaws (WAM P.2503) in the Western Australian Museum, and from the dental formula

$\frac{13-2-13}{13-1-13}$ and the shape of the teeth I have no hesitation in referring them to *amblyrhynchos*. I have also seen the photographs in the

Australian Museum, from one of which Whitley traced his outline drawing of *fowleri* (his figure 2), and I have no doubt that the shark in these photographs is another species, *brevipinna*. Whitley regarded the jaws and the photographs as being the holotype of *fowleri*, but this cannot be maintained because they represent two different species. Accordingly, as discussed in more detail in my account of *brevipinna* (p. 43), I designate the jaws as operative holotype of *fowleri*, and in so doing I refer *fowleri* to the synonymy of *amblyrhynchos*.

Galeolamna tufiensis, described by Whitley (1949, 1951a) from Papua, is synonymized here with *amblyrhynchos* but with some reservation and to a certain extent by elimination. In his first notice of the species, Whitley (1949) regarded it as allied to *nesiotes* (= *amblyrhynchos*) but differing in having a smaller second dorsal fin. In his later account (1951a) Whitley gave measurements of the holotype and four paratypes of *tufiensis*, which ranged from 673 to 2,545 mm TL. From these measurements the length of the second dorsal fin base ranged from 3.5 to 5.1% (mean 4.0%) TL, while the posterior margin of the same fin was from 3.2 to 4.2% (mean 3.7%). In 10 specimens of *amblyrhynchos* which I have measured (see Table 52), the second dorsal fin base ranges from 4.0 to 4.5% (mean 4.3%) TL, and the posterior margin from 3.7 to 4.8% (mean 4.2%). These figures lend some support to Whitley's view of the distinctness of *tufiensis*, but considering the degree of overlap of the measurement ranges, and possible differences in the methods of making the measurements, I hesitate to use them as definite evidence for retaining *tufiensis* as a separate species. The only type material of *tufiensis* that was preserved are some individual teeth in the Australian Museum; these agree well with *amblyrhynchos*. Further consideration of the status of *tufiensis* can only be made on Whitley's second account (1951a) of the species, which includes a line drawing (his figure 1) showing the holotype in lateral view. Most features of this account accord with *amblyrhynchos* but there are some that disagree. In Whitley's illustration the eye is shown well behind the front of the mouth, virtually above the jaw angles. This is an unusually rearward position for any species of *Carcharhinus*. In my material of *amblyrhynchos* the anterior edge of the eye is just forward of the front of the mouth. Whitley gave the dental formula of the holotype of *tufiensis* as $\frac{10?-1-11}{13-1-12}$, and of two paratypes as

$\frac{12-1-13}{13-1-13}$ and $\frac{13-1-13}{10-1-13}$. All of my material of *amblyrhynchos* have counts within the range $\frac{13 \text{ or } 14-1 \text{ or } 2-13 \text{ or } 14}{13 \text{ or } 14-1-13 \text{ or } 14}$. The variation in

Whitley's formulae, not only between different specimens but also between different sides of the jaw in the same specimen, is rather more than normal in *Carcharhinus* species, suggesting that the counts were made with the jaws in situ and hence increasing the likelihood that some of the smaller teeth at the side of the jaw were overlooked. Lastly, Whitley described the fins of *tufiensis* as being "dark grey above" but did not mention any dusky to black edging along the posterior margin of the caudal fin—a feature which is usually conspicuous in *amblyrhynchos*. Because of these discrepancies, final evaluation of the status of *tufiensis* must await further material.

Table 52.—*Carcharhinus amblyrhynchos*, proportional dimensions in percentage of total length.

	♂ 600 mm Marshall Is. Rongerik Atoll USNM 140968	♂ 611 mm New Guinea Port Moresby USNM 39991	♀ 621 mm Philippines off Luzon Point USNM 151232	♀ 645 mm Solomons New Georgia USNM 114623	♀ 645 mm Australia Queensland USNM 176717	♂ 670 mm Philippines off Luzon Point USNM 151232	♀ 703 mm Solomons New Georgia USNM 114627	♂ 735 mm Solomons New Georgia USNM 114626	♀ 853 mm Marshall Is. Eniwetok Atoll USNM 140967	♀ 930 mm Marshall Is. Bikini Atoll USNM 140966
Snout tip to										
outer nostrils	3.7	3.2	3.1	4.2	3.7	3.5	3.7	3.7	3.3	3.7
eye	7.8	6.7	7.0	7.8	8.1	7.5	8.1	8.0	7.6	7.6
mouth	8.7	7.2	7.8	8.7	8.5	8.2	8.4	8.6	8.1	8.1
1st gill opening	21.0	18.3	19.1	20.9	19.4	19.5	20.5	21.2	20.7	21.0
3d gill opening	23.0	20.4	21.1	22.6	22.0	21.6	—	24.1	23.0	23.0
5th gill opening	24.7	22.1	22.7	24.0	24.1	23.1	24.7	26.0	24.7	24.9
pectoral origin	23.3	21.3	21.7	22.6	22.9	21.9	23.6	24.9	23.1	23.8
pelvic origin	48.8	47.4	48.4	47.3	46.5	48.1	48.1	50.0	50.9	49.6
1st dorsal origin	32.4	31.4	30.9	31.8	31.0	31.0	31.2	33.0	32.3	32.2
2d dorsal origin	62.2	59.8	58.8	59.1	59.7	60.4	59.9	61.8	61.0	62.3
anal fin origin	62.5	60.5	59.2	59.2	60.2	60.3	59.9	61.8	61.4	61.1
upper caudal origin	73.4	71.2	70.8	70.9	71.0	72.0	71.2	73.4	73.0	73.1
lower caudal origin	72.9	70.4	70.1	70.0	70.1	71.7	70.2	72.9	72.3	72.6
Nostrils										
distance between inner corners	6.3	5.7	6.2	6.8	6.2	6.4	6.5	6.7	6.3	6.2
Mouth										
width	8.3	7.7	7.7	9.3	9.2	8.8	9.5	9.3	9.2	9.5
length	5.8	5.7	4.9	5.4	5.1	5.1	5.8	6.0	5.6	5.4
Labial furrow lengths										
upper	0.7	0.3	0.3	0.5	0.5	0.4	0.5	0.4	0.6	0.5
lower	0.7	0.3	0.4	0.5	0.4	0.4	0.4	0.5	0.6	0.4
Gill opening lengths										
1st	2.4	—	2.4	2.7	3.0	2.6	2.8	3.4	3.0	3.1
3d	2.8	—	2.8	3.1	3.4	3.1	3.2	4.2	3.5	3.9
5th	2.2	—	2.3	2.5	2.6	2.6	2.2	3.3	2.5	2.7
Eye										
horizontal diameter	2.7	2.8	2.7	2.6	2.6	2.6	2.6	2.6	2.2	2.0
1st dorsal fin										
length of base	8.5	10.0	8.9	9.6	9.3	9.5	9.2	10.2	9.8	10.0
length posterior margin	3.7	3.8	3.5	3.9	4.0	4.3	4.3	3.8	4.2	4.7
height	10.3	10.8	10.9	9.3	10.7	10.7	9.1	10.9	9.7	10.1
2d dorsal fin										
length of base	4.0	4.4	4.2	4.2	4.2	4.5	4.2	4.5	4.2	4.3
length posterior margin	3.7	3.8	4.2	4.2	4.2	3.9	4.5	4.1	4.2	4.8
height	2.7	3.1	3.1	3.1	3.1	3.0	3.4	3.1	3.0	3.1
Anal fin										
length of base	4.3	4.1	4.8	4.3	4.2	5.5	4.3	5.5	4.2	4.3
length posterior margin	3.4	3.5	3.6	3.7	3.9	3.9	4.3	3.7	3.6	4.4
height	3.2	3.1	2.9	3.4	3.1	3.0	3.8	3.7	3.2	3.3
Pectoral fin										
length of base	5.7	4.7	4.7	5.7	5.6	5.5	5.5	5.8	6.1	6.1
length anterior margin	18.7	18.8	19.0	18.9	18.6	19.5	19.6	20.5	19.8	19.3
length distal margin	14.7	14.4	15.0	16.0	14.7	16.1	18.6	17.0	16.0	16.9
greatest width	8.7	9.0	8.7	8.5	9.1	—	9.8	9.5	10.0	10.2
Pelvic fin										
length of base	5.0	4.6	4.3	4.7	5.1	5.2	5.0	5.0	5.2	4.8
length anterior margin	5.5	5.2	5.3	5.4	5.7	5.5	5.0	5.4	5.7	5.6
length distal margin	5.0	4.7	4.7	5.0	5.3	5.2	5.5	5.2	5.5	5.8
length of claspers	2.1	1.8	—	—	—	1.8	—	2.0	—	—
Caudal fin										
length of upper lobe	28.6	29.1	29.6	29.8	29.2	29.2	28.6	27.6	26.5	26.7
length of lower lobe	13.3	14.7	14.6	13.9	14.1	14.0	14.4	14.3	13.3	14.4
Trunk at pectoral origin										
width	11.2	10.5	10.9	13.6	12.7	11.9	12.8	12.8	12.4	12.9
height	8.5	9.0	10.9	9.8	10.4	10.7	11.4	12.8	10.9	11.3
Dental formula	14-1-14 14-1-14	14-1-14 14-1-14	14-1-14 13-1-13	14-1-14 13-1-13	14-1-14 13-1-13	14-1-14 13-1-13	14-1-14 13-1-13	14-1-14 13-1-13	13-1-13 13-1-13	13-1-13 13-1-13
Vertebrae										
precaudal	115	117	116	114	116	111	115	115	115	118
caudal	99	104	99	99	103	103	100	100	97	96
total	214	221	215	213	219	214	215	215	212	214

Galeolamna coongoola Whitley, from off Queensland, Australia, can fairly confidently be ascribed to *amblyrhynchos* on the basis of Whitley's account (1964). Type material is fragmentary, consisting only of teeth and skin samples from the holotype, and of the same plus a pelvic fin and clasper from the paratype (Whitley's allotype). The teeth, in the Australian Museum, agree closely with *amblyrhynchos*, as do the dental formulae given by Whitley. The illustration of the holotype does, however, show the eye slightly behind the front of the mouth, but Whitley's measurements (1964) indicate the reverse for the paratype. Whitley regarded *coongoola* as differing from *tufiensis* in having a larger second dorsal fin. This difference, which would bring *coongoola* more into line with *amblyrhynchos*, is not well borne out by his measurements of the two type specimens of *coongoola* (Whitley 1964) in which the second dorsal base is 3.8 and 3.9% TL, and the posterior margin is 4.6 and 3.7% (for comparison with *tufiensis* and with my measurements of *amblyrhynchos* see above). Whitley also measured the anterior margin of the second dorsal fin—in the *coongoola* types this was 4.8 and 3.7% TL, whereas in the five *tufiensis* type specimens it ranged from 4.2 to 5.7% (mean 4.7%). The only disquieting feature between the description of *coongoola* and my material of *amblyrhynchos* is the color pattern. Whitley stated that *coongoola* has "No conspicuous dark or light tips to fins," and also did not mention any dark edging posteriorly on the caudal fin. However, Whitley kindly supplied me with a photograph labelled "Probably IB 6009" which seemingly is the paratype of *coongoola*, and this shows the characteristic color pattern of *amblyrhynchos*, including the dark edging on the posterior of the caudal fin. On this basis, plus also the fact that I have seen one other specimen of *amblyrhynchos* from Queensland, I believe that *coongoola* is conspecific with *amblyrhynchos*.

Description (see also Table 52).—Large sharks, growing to at least 2.5 m TL. Midline of back between dorsal fins smooth, lacking an interdorsal ridge in many preserved specimens and perhaps in all in life, but with a faint to moderately developed low dermal ridge in some preserved specimens, possibly as an artifact from preservation. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles close-packed, overlapping, subcircular in outline in small specimens, more nearly rhomboid in larger, each with three or five strong longitudinal ridges and corresponding sharp-pointed but short posterior marginal teeth in small specimens, seven in larger.

Snout moderately long and moderately rounded in contour. Anterior margin of eye is slightly forward of front of mouth. Nostrils strongly oblique, slitlike, the anterior margin of each with a low, pointed lobe.

Dental formula $\frac{14-1-14}{13-1-13}$ in 7 of 15 specimens counted; $\frac{13-1-13}{13-1-13}$ in 4; $\frac{14-1-14}{14-1-14}$ in 2; $\frac{14-1-14}{14-1-13}$ or $\frac{13-2-14}{14-1-13}$ in the holotype of *amblyrhynchos*; and $\frac{13-2-13}{13-1-13}$ in the holotype of *nesiotes*. Upper teeth moderately narrow, oblique except for the first two series on

each side of symphysis, their lateral margins concave to notched, their medial margins weakly concave to sinuous or almost straight, both margins coarsely serrated, the serrations noticeably larger basally on the lateral margins; one, occasionally two, small symphyseal teeth. Lower teeth narrow, erect except for the most lateral three or four series, both margins concave to almost notched basally, smooth edged in small specimens but very weakly serrated on the more lateral teeth of larger specimens; one small symphyseal tooth.

First dorsal fin moderately high, its apex acute to sharply rounded; origin of first dorsal just anterior to or over inner (posterior) corner of pectoral fin. Second dorsal fin moderately high and long, almost equal to anal fin; length of second dorsal rear tip 1.2-1.6 times second dorsal height; origin of second dorsal about over anal fin origin. Pectoral fins noticeably long, slender; origin of pectorals below and between the levels of the third and fourth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches behind level of first dorsal axil to as far as first dorsal rear tip.

Color in life was described by Schultz (1953, as *menisorrah*), as "... a narrow blackish band can be seen on posterior edge of upper lobe of caudal fin; back and upper sides grayish-black; fins generally grayish, becoming blackish distally but not 'black-tipped'; pectorals notably blackish above and on under sides, except central and basal parts, which are paler." After preservation in alcohol this color pattern remains, though the back and sides are dark grayish brown. The overall appearance is notably dusky, accentuated by the darker fins. The first dorsal fin is much less dusky than the other fins, and is usually plain colored although occasionally its trailing margin has a narrow and irregular white edging near the apex.

Vertebral counts of 10 specimens are given in Table 52 and of another 3 specimens in Table 53. Bass et al. (1973) reported a precaudal count of 114 and a total count of 212 from one specimen off the northwest coast of Madagascar.

Centrum diameter considerably greater than centrum length even in longest monospondylous centra at posterior of abdomen.

Diplospondylous centrum length regular. Diplospondyly begins above anterior to middle of pelvic base. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.56-0.67 (mean 0.61) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.08-1.19 (mean

1.15) in 12 specimens, but 1.32 in a Solomon Islands specimen (USNM 114627).

The smallest, apparently free-living specimen I have seen was 600 mm TL, while the largest embryo was 590 mm. I have seen only juvenile males, the largest 735 mm TL; however, the paratype male of *coongoola*, 1,448 mm TL, was recorded by Whitley (1964) as having a clasper length equal to 9.1% TL, and hence would be mature, while the largest male paratype of *tufiensis*, 2,545 mm TL, was

Table 53.—Vertebral numbers in three specimens of *Carcharhinus amblyrhynchos*.

Specimens		Precaudal	Caudal	Total
USNM 140968	Marshall Islands	116	95	211
GVF 99	Tuamotu Archipelago	119	95	218
GVF 2467	Gulf of Thailand	110	107	217
Range (including counts from Table 52)		110-119	95-107	211-221

similarly recorded by Whitley (1951a) as having a clasper length of 10.2% TL. Data from Wass (*in* Bass et al. 1973) for Hawaiian males gave their size at maturity at about 1,300-1,350 mm. Bonham (1960) reported that two females, 1,220 and 1,370 mm TL, from the Marshall Islands were immature, whereas another of 1,410 mm contained three embryos. Whitley (1951a) described the female holotype of *tufiensis*, 1,481 mm TL, as "spent." Schultz (1953) listed three pregnant females from the Marshall Islands, two containing two embryos, and the third with only one embryo; total lengths of these females were not given. Tester (see footnote 4) recorded five pregnant females from the Hawaiian Islands; embryo numbers ranged from three to six and averaged five. The largest specimen measured by Schultz (1953) was a female of 2,325 mm TL. The large male paratype of *tufiensis*, 2,545 mm TL, seems to be the maximum size so far reported. Whitley's report (1951a) of a female, about 2,800 mm, which he tentatively identified as *tufiensis*, seems doubtful as *amblyrhynchos* since it was said to contain about a dozen embryos—a far higher number than any of the others mentioned above. In an extensive sample (274 specimens) from Hawaiian waters, maximum lengths were much shorter, being only 1,740 mm (male) and 1,870 mm (female) according to Wass (*in* Bass et al. 1973).

Distribution (see also Material examined).—Based on specimens I have examined, *amblyrhynchos* has a wide distribution in the central Pacific and westwards to the eastern Indian Ocean. My most eastern records are from the Tuamotu Archipelago in the south, and the Hawaiian Islands in the north. Westward from these localities, *amblyrhynchos* occurs at the Cook Islands, the Phoenix Islands, the Marshall Islands, the Solomon Islands, Lord Howe Island, New Guinea, the Philippine Islands, the Java Sea, and on both coasts of Australia (Queensland and Western Australia). I have also seen one specimen from India (no other locality data). Published records for other Pacific localities and seemingly referable to *amblyrhynchos* include those of Bleeker (1861)—Singapore; Randall (1955)—Gilbert Islands; Church (1961)—Wake Island; Fellows and Murchison (1967)—Johnston Island; Read (1969)—Caroline Islands; Randall (1973)—Pitcairn Island and associated Oeno Atoll; and Bryan (1973)—Guam Island. Tang (1934) listed the species from China, but I have not seen his account. At variance with the distributional picture set by the above records, or at least greatly extending the known range of *amblyrhynchos*, is Bass et al.'s (1973) report of one juvenile specimen from the northwest coast of Madagascar. Their detailed account of this specimen agrees in all respects with *amblyrhynchos*, and they discussed the differences between *amblyrhynchos* and the very similar *wheeleri* which they also reported (as *spallanzani*) and which is common in the western Indian Ocean. The significance of this range extension (i.e., whether it can be interpreted as a reflection of the normal distribution of *amblyrhynchos* or whether it is due to an ephemeral straggler population) cannot yet be determined. Records definitely not applying to *amblyrhynchos* include those of Ogilby (1915) from Queensland whose material is referable to *amblyrhynchoides*, and of Giltay (1933) from the Aru Islands (Arafura Sea).

Material examined.—SOSC Ref. No. 203, female embryo, 515 mm, Phoenix Islands, 29 May 1965; BMNH 1889.2.1.4176, female embryo, 590 mm, India, F. Day; USNM 140968, two juvenile males, 600 and 650 mm, Marshall Islands, Rongerik Atoll, 1 mi off Rongerik Island, 16-28 June 1946, L. P. Schultz and crew of *Bowditch*; USNM 39991, juvenile male, 611 mm, New Guinea, Port Moresby; USNM 151232, juvenile female, 621 mm, and male, 670 mm, Philippine Islands, off Luzon Point, 31 January and 7 February 1909, *Albatross*; GVF Reg. No. 2467, juvenile male, 641 mm, Gulf of Thailand, Trat Province, about 2-3 mi offshore, W and WSW of Goh Chang, ca. 11°56' to 12°03' N, 102°14'30" to 102°17'45" E, (via Bangkok Fish Market), 12 January 1961; USNM 114623, juvenile female, 645 mm, Solomon Islands, New Georgia, 1944, W. M. Chapman; USNM 176717, juvenile female, 645 mm, Australia, Queensland, Great Barrier Reef near Brisbane, 8 April to 29 May 1952, University of Miami, Department of Zoology; USNM 114627, female, 703 mm, Solomon Islands, New Georgia, Wana Wana Island, 22 May 1944, W. M. Chapman; GVF Reg. No. 99, female, 724 mm, Tuamotu Archipelago, Raroia Island, 25 July 1952, R. R. Harry and others; AMS IA.1285, female, 735 mm, Lord Howe Island, December 1922, R. Baxter; USNM 114626, immature male, 735 mm, Solomon Islands, New Georgia, Wana Wana Island, June 1944, W. M. Chapman; DM 4618, female, 840 mm, Cook Islands, Palmerston Island, 1960, J. C. Burland; USNM 140967, female, 853 mm, Marshall Islands, Eniwetok Atoll, SW passage, 26-30 May 1946, L. P. Schultz et al.; USNM 140966, female, 930 mm, Marshall Islands, Bikini Atoll, Bokoro Channel, 6 April 1946, L. P. Schultz and V. E. Brock; AMS IB.6006, teeth and skin fragments of female, 940 mm (holotype of *Galeolamna coongoola*), Australia, Queensland, Swain Reefs, Gillett Cay, 14 October 1962; AMS IB.6009, some teeth, skin fragments, and pelvic fin with clasper of male, 1,448 mm (paratype of *Galeolamna coongoola*), Australia, Queensland, Swain Reefs, Capre Cay, 22 October 1962, R. Marshall; USNM 50860, head and skin of female, 1,480 mm (holotype of *Carcharias nesiotes*), Hawaiian Islands, French Frigate Shoals, 1902, *Albatross*; AMS IB.2334, two upper and seven lower teeth of female, 1,481 mm (holotype of *Galeolamna tufiensis*), Papua, off Tufi Harbor, 1 October 1948, *Fairwind*; RNH 7377, head and skin of female, ca. 1,540 mm [holotype of *Carcharias (Prionodon) amblyrhynchos*], Java Sea near Solombo Islands, P. Bleeker; WAM P.2503, jaws (holotype of *Galeolamna fowleri*) supposedly from male, ca. 1,675 mm, Western Australia, Exmouth Gulf, South Muiron Island, 20 October 1943, S. Fowler.

Carcharhinus wheeleri n. sp. Figures 50, 51

Diagnosis.—Moderate-sized sharks, up to 1.72 m long, usually lacking an interdorsal ridge; apical tip and trailing margin of first dorsal fin white; trailing margin of caudal fin prominently edged with black; tips and trailing margins of other fins dusky to black; snout moderately short and bluntly rounded; internarial width 1.0-1.3 in preoral length; origin of first dorsal fin over or just anterior to inner pectoral corner; apex of first dorsal sharply rounded to acute; origin of second dorsal in front of or over anal fin origin; height of second dorsal 2.8-4.1% TL and 1.0-1.5 in length of its rear tip; dental formula usually $\frac{13-1-13}{12 \text{ or } 13-1-12 \text{ or } 13}$ but may be

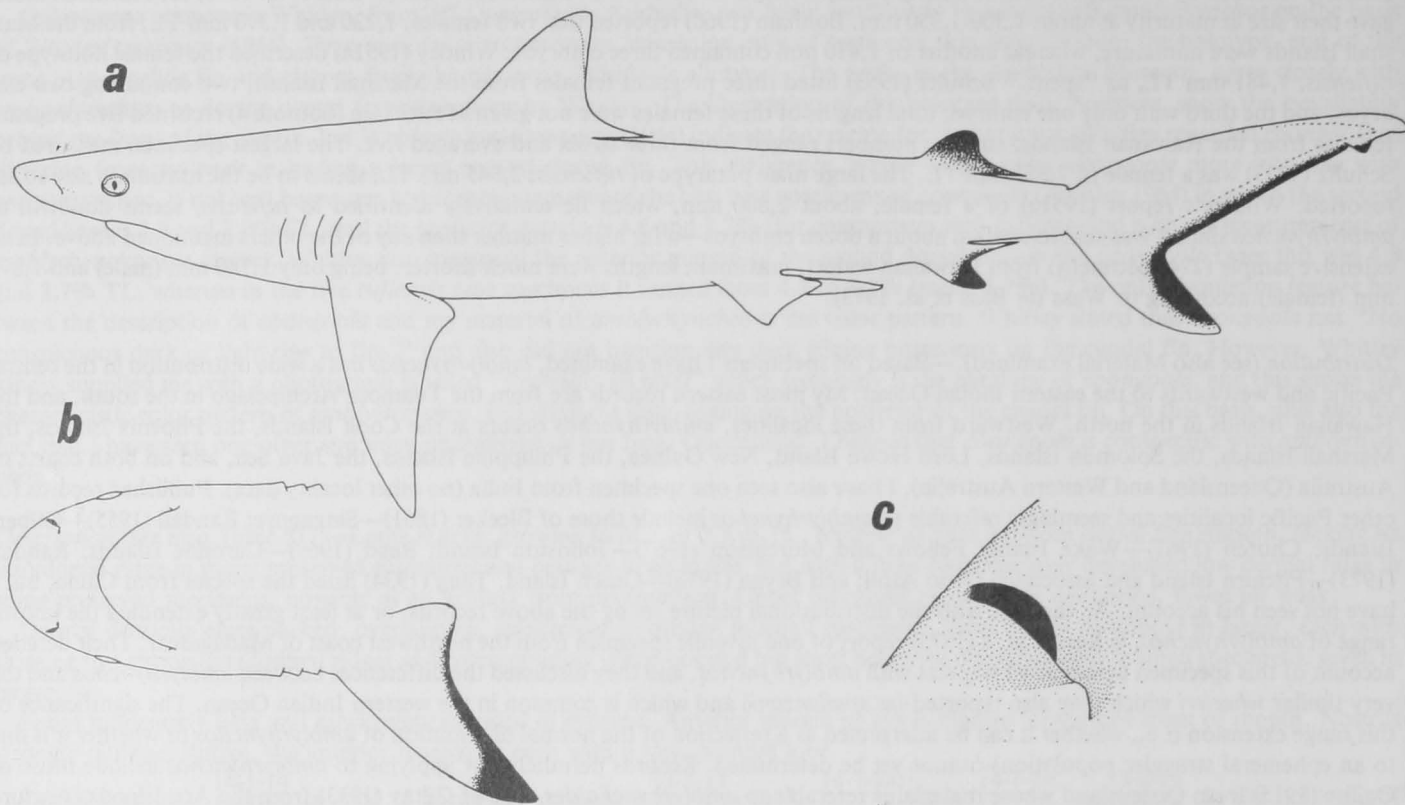


Figure 50.—*Carcharhinus wheeleri* n. sp., holotype, USNM 197418, 1,322 mm TL, male from Red Sea: *a*, left side (dotted line towards apex of first dorsal fin indicates extent of white mark on tip); *b*, underside of head; *c*, enlarged left nostril.

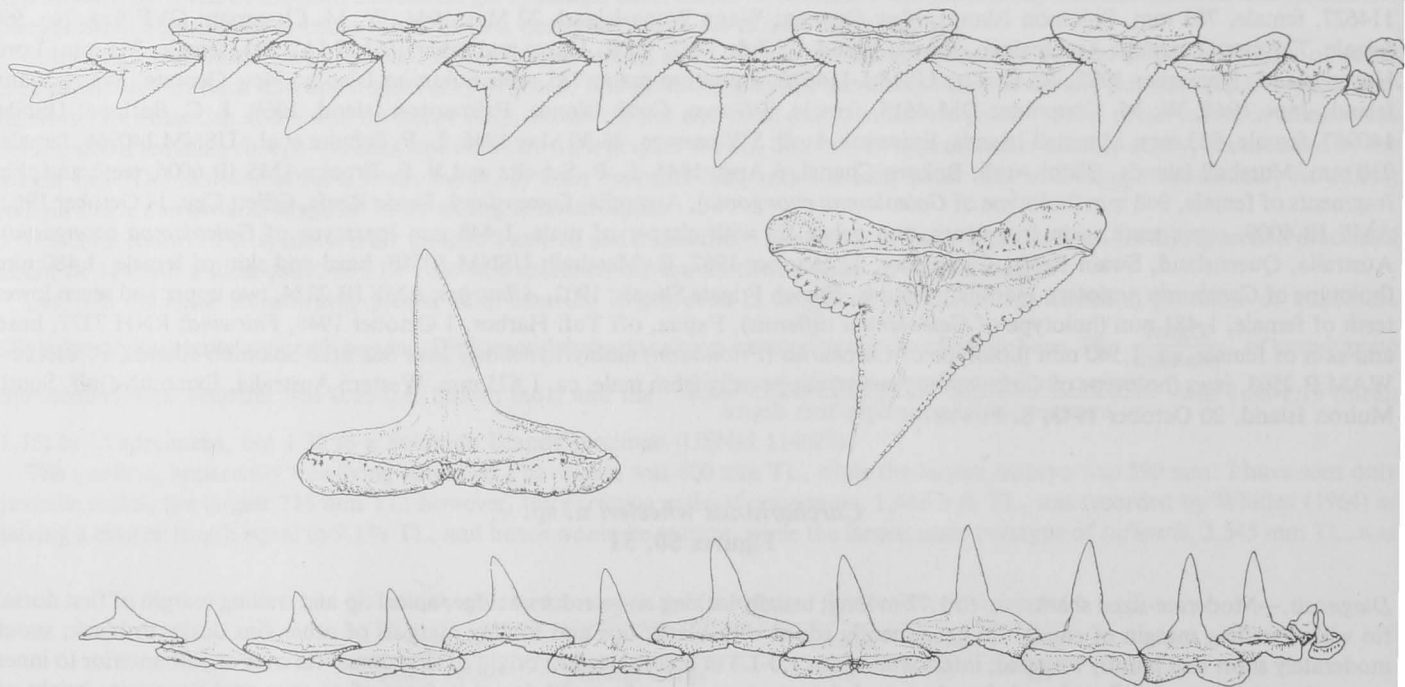


Figure 51.—*Carcharhinus wheeleri* n. sp., holotype, USNM 197418, 1,322 mm TL, male from Red Sea: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

13 or 14-1 or 2-13 or 14
12 or 13-1-12 or 13 ; upper teeth moderately narrow, oblique, concave to notched laterally, with slightly coarser serrations basally; lower teeth erect, serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 110-117; caudal centra 102-112; total centra 210-227; diplospondyly begins from one-third to halfway along pelvic base; diplospondylous centra regular in length; penultimate monospondylous centrum 1.6-1.8 times wider than long.

This western Indian Ocean-Red Sea species is very similar to the Indo-Pacific *amblyrhynchos* but differs in having a white-tipped first dorsal fin, shorter prenarial and preoral lengths, and usually in having one less tooth on each side of the upper jaw. None of these characters is exclusive. Prenarial and preoral proportions overlap (Table 54, Fig. 52).

Table 54.—Proportional dimensions indicating differences between *Carcharhinus wheeleri* and *C. amblyrhynchos*.

Species	Prenarial length as % TL		Preoral length as % TL		Preoral Prenarial		No. of specimens	Size range (TL, mm)
	Range	Mean	Range	Mean	Range	Mean		
<i>wheeleri</i>	2.4-3.2	2.8	6.4-7.9	7.2	2.4-2.9	2.6	8	521-1,322
<i>amblyrhynchos</i>	2.4-4.2	3.5	5.8-8.7	8.0	2.1-2.6	2.3	15	600-1,540

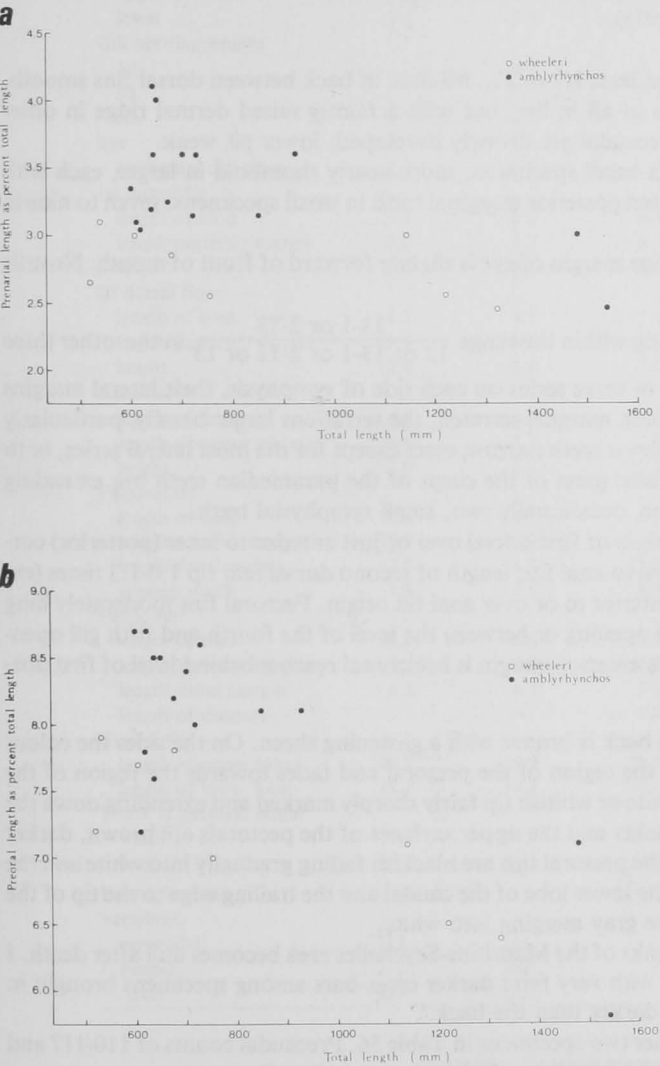


Figure 52.—Proportional dimensions indicating differences between *Carcharhinus wheeleri* n. sp. and *C. amblyrhynchos*: a, prenarial length as percent of total length versus total length; b, preoral length as percent of total length versus total length.

The white marking on the first dorsal was present on all specimens of *wheeleri* examined by me, and was noted also in the descriptions by Fourmanoir (1961), Wheeler (1963), and Bass et al. (1973) of their western Indian Ocean material. In contrast to this I did not observe white markings on any of the numerous specimens of *amblyrhynchos* from the Indo-Pacific which I saw during the course of

the study. However, recently Fourmanoir¹⁸ advised me that one of two specimens of *amblyrhynchos* caught together at New Caledonia had a white-edged first dorsal, and likewise Johnson¹⁹ provided data and dorsal fins from white-marked specimens from the Tuamotu Archipelago. Johnson noted that "this tendency for a very small percent of the local population of *C. amblyrhynchos* to possess white fringed first dorsals is within the range of normal diversity for the species. None of these specimens, however, have possessed as notable a white-fringed first dorsal as that pictured" [in the color photograph of a Red Sea specimen in Doubilet (1975)]. The two dorsal fins sent by Johnson confirm this latter observation—the white edging on the trailing margin is much less regular, narrower, and extends onto less of the apex of the fin than in *wheeleri*. Moreover, Johnson advised that his white-marked Tuamotu specimens did not differ in preoral length from normal *amblyrhynchos*, thus contrasting with the shorter snouted *wheeleri*.

Although the above evidence does not lend unequivocal support to my proposal that *wheeleri* should be recognized as a separate species, it does not negate it insofar as all the specimens concerned were still able to be ascribed either to *wheeleri* or to *amblyrhynchos*. Other support, albeit meager, for upholding *wheeleri* is the limited sympatry of the two species evidenced by Bass et al.'s (1973) account of one specimen of *amblyrhynchos* from off the northwest coast of Madagascar, and the suggestion of behavioral differences given in the caption to the photograph of *wheeleri* in Doubilet (1975) which states the "Though resembling the aggressive Indo-Pacific gray reef shark [= *amblyrhynchos*], it behaves quite differently, fleeing if confronted by a diver."

Nomenclatural discussion.—This species, which is common in the western Indian Ocean and is present also in the Red Sea, has been reported under several different names, but none of these is available for it. The new specific name proposed for it here is in honor of J. F. G. Wheeler, formerly Director of the East African Marine Fisheries Research Organization, whose 1953 account of it, as *Carcharhinus amblyrhynchos*, from the Mauritius-Seychelles area is the first definite record that I have been able to find. In a later and fuller account, Wheeler (1963) recognized it as *amblyrhynchus* but without giving reasons for the emendation of the name. The species has also been reported by Fourmanoir (1961) as *amblyrhynchus*, by Klauswitz (1959) as *menisorrah*, and by D'Aubrey (1964) and Bass et al. (1973) as *spallanzani*. A fuller synonymy, including citations as *bleekeri* and *leucas*, is given in Bass et al. (1973). An underwater color photograph of a Red Sea specimen is reproduced in Doubilet (1975).

Description (see also Table 55).—Moderately large sharks, growing to at least 1.7 m TL. Midline of back between dorsal fins smooth, lacking an interdorsal ridge in some preserved specimens and perhaps in all in life, but with a faintly raised dermal ridge in other preserved specimens, possibly an artifact from preservation. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles close-packed, overlapping, subcircular in outline in small specimens, more nearly rhomboid in larger, each with three to five longitudinal ridges and corresponding short but sharp-pointed posterior marginal teeth in small specimens, seven to nine in larger.

Snout moderately short and rather bluntly rounded in contour. Anterior margin of eye is slightly forward of front of mouth. Nostrils strongly oblique, slitlike, the anterior margin of each with a low lobe.

Dental formula $\frac{13-2-13}{12-1-12}$ in three of six specimens counted, and falling within the range $\frac{13-1 \text{ or } 2-13}{12 \text{ or } 13-1 \text{ or } 2-12 \text{ or } 13}$ in the other three specimens. Upper teeth rather narrow, oblique except for the first two or three series on each side of symphysis, their lateral margins concave to notched, their medial margins weakly concave to sinuous, both margins serrated, the serrations larger basally, particularly on the lateral margins; two, occasionally one, small symphyseal teeth. Lower teeth narrow, erect except for the most lateral series, both margins concave, weakly serrated, the serrations only on the tips or distal parts of the cusps of the paramedian teeth but extending down onto the bases in the teeth toward the corners of the mouth; one, occasionally two, small symphyseal teeth.

First dorsal fin moderately high, its apex acute to sharply rounded; origin of first dorsal over or just anterior to inner (posterior) corner of pectoral fin. Second dorsal fin moderately high and long, subequal to anal fin; length of second dorsal rear tip 1.0-1.3 times (exceptionally 1.5) second dorsal height; origin of second dorsal slightly anterior to or over anal fin origin. Pectoral fins moderately long and noticeably narrow distally; origin of pectorals below the fourth gill opening or between the level of the fourth and fifth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches behind level of first dorsal axil to as far as first dorsal rear tip.

Color was described by Wheeler (1963) as "When freshly caught the back is bronze with a glistening sheen. On the sides the colour fades into white. A broad strip of bronze passes obliquely down from the region of the pectoral and fades towards the region of the pelvis. The first dorsal fin is brown or bronze like the back but has a white or whitish tip fairly sharply marked and extending down the trailing edge. The second dorsal is brown like the back or somewhat darker and the upper surfaces of the pectorals are brown, darker than the back, and merging into blackish at the tips. The undersides of the pectoral tips are blackish fading gradually into white and the trailing edges of these fins are also edged with black. The lower part of the lower lobe of the caudal and the trailing edge to the tip of the dorsal lobe are blackish. The free edges of the anal and pelvics may be gray merging into white.

"The rich bronze or copper colour of the fresh specimens from the banks of the Mauritius-Seychelles area becomes dull after death. I have records of pale blue grey, pale brown grey, greyish olive and grey with very faint darker cross-bars among specimens brought in from East African waters with all the fins except the white tipped DI darker than the back."

Vertebral counts of four specimens are given in Table 55 and of another two specimens in Table 56. Precaudal counts of 110-117 and total counts of 210-220 were reported by Bass et al. (1973) for nine specimens from the southwest Indian Ocean.

¹⁸P. Fourmanoir, Office de la Recherche Scientifique et Technique Outre-Mer, Centre de Noumea, B.P. No. 4, Noumea, New Caledonia, pers. commun. February 1977.

¹⁹R. Johnson, Director, S.E.A. Institute, Inc., 2018 Pacific Ave., Long Beach, CA 90806, pers. commun. January 1977.

Table 55.—*Carcharhinus wheeleri* n. sp., proportional dimensions in percentage of total length.

	♀ 521 mm Réunion MNHN 8001	♀ 539 mm Gulf of Aden BMNH 1925. 7.20.7	♂ 607 mm Red Sea NMV 61.441	♂ 677 mm Red Sea NMV 61.441	♂ 757 mm Red Sea NMV 61.448	♀ 1,145 mm Red Sea NMV 61.446	♂ 1,220 mm Red Sea NMV 61.441	♂ 1,322 mm Red Sea USNM 197418
Snout tip to								
outer nostrils	2.8	3.2	3.0	2.7	2.6	3.0	2.6	2.4
eye	7.0	7.5	7.1	6.9	6.6	6.9	6.2	6.3
mouth	7.2	7.9	7.7	7.8	7.0	7.1	6.5	6.4
1st gill opening	18.6	19.2	20.3	19.5	19.0	18.8	19.3	19.7
3d gill opening	20.8	21.4	22.3	21.7	21.1	21.6	21.7	22.3
5th gill opening	22.1	23.3	24.3	23.6	22.7	23.5	23.7	24.2
pectoral origin	21.8	22.3	23.6	23.3	21.8	23.1	22.8	23.4
pelvic origin	46.9	46.2	48.5	49.0	46.5	52.1	49.7	50.3
1st dorsal origin	29.3	29.3	30.4	31.2	29.9	31.6	31.4	31.1
2d dorsal origin	58.4	57.4	59.6	64.4	59.2	63.7	63.4	64.6
anal fin origin	59.2	58.8	60.1	64.8	59.3	63.9	63.7	64.8
upper caudal origin	—	70.1	71.7	71.7	70.7	75.1	74.9	76.5
lower caudal origin	69.2	69.1	70.7	70.7	70.2	74.5	74.4	75.9
Nostrils								
distance between inner corners	5.6	6.1	6.4	6.6	5.9	7.1	6.7	6.4
Mouth								
width	7.5	7.6	8.1	8.7	7.8	10.8	9.6	9.9
length	5.0	5.0	5.3	5.2	5.0	5.5	5.3	5.3
Labial furrow lengths								
upper	0.5	0.5	0.4	0.4	0.4	0.4	0.4	0.5
lower	0.4	0.5	0.5	0.5	0.5	0.5	0.8	0.5
Gill opening lengths								
1st	2.3	2.6	2.3	3.0	2.5	2.9	2.5	2.9
3d	2.7	3.1	2.5	3.1	2.9	3.2	3.0	3.3
5th	2.2	2.4	2.0	2.4	2.6	2.5	2.5	2.6
Eye								
horizontal diameter	2.9	2.9	2.8	2.9	2.4	2.1	2.0	1.9
1st dorsal fin								
length of base	9.4	10.2	9.6	9.3	8.3	9.6	9.2	10.2
length posterior margin	3.6	3.3	4.1	4.1	4.1	5.1	4.3	4.7
height	8.6	8.6	10.6	10.6	10.7	10.5	9.0	8.9
2d dorsal fin								
length of base	4.2	4.8	3.6	4.1	4.1	4.2	3.9	4.2
length posterior margin	3.5	3.3	3.9	4.4	3.8	4.5	4.0	4.2
height	2.9	2.8	3.6	3.0	3.7	4.1	3.3	3.2
Anal fin								
length of base	4.0	4.4	4.0	4.4	4.0	4.6	4.7	4.0
length posterior margin	3.4	3.3	3.6	4.0	3.8	4.1	3.9	3.7
height	3.0	3.1	3.1	3.8	3.7	4.3	3.5	3.2
Pectoral fin								
length of base	4.9	4.8	5.1	5.3	5.0	6.3	5.5	5.8
length anterior margin	17.9	17.9	19.0	18.2	18.2	21.4	18.3	18.2
length distal margin	12.2	11.9	15.2	15.5	14.7	18.6	14.6	15.4
greatest width	7.9	8.5	8.6	9.0	10.8	10.3	9.3	9.2
Pelvic fin								
length of base	4.8	5.0	4.6	4.7	4.8	5.4	5.4	5.6
length anterior margin	5.5	5.9	4.9	4.9	4.8	6.0	5.1	5.4
length distal margin	4.4	4.7	5.1	5.6	5.2	6.8	5.0	5.6
length of claspers	—	—	1.8	1.8	1.7	—	7.3	7.5
Caudal fin								
length of upper lobe	29.2	29.9	28.9	28.8	29.8	26.5	25.7	23.8
length of lower lobe	14.2	14.1	15.0	13.8	14.4	15.5	13.3	13.0
Trunk at pectoral origin								
width	11.2	11.1	10.9	11.7	10.5	14.9	12.7	12.3
height	10.4	11.5	9.7	10.8	9.3	—	10.9	12.1
Dental formula			13-2-13 12-1-12	13-1-13 12-1-12	13-1-13 13-1-13		13-1-13 12-1-12	13-2-13 12-2-12
Vertebrae								
precaudal	115	111			114			115
caudal	112	102			103			102
total	227	213			217			217

Table 56.—Vertebral numbers in two specimens of *Carcharhinus wheeleri*.

Specimens	Precaudal	Caudal	Total
ISZZ 10687 Red Sea	116	108	224
USNM 197675 Kenya	112	—	—
Range (including counts from Table 55)	111-116	102-112	213-227

Centrum diameter considerably greater than centrum length even in longest monospondylous centra at posterior of abdomen. Diplospondylous centra regular, and only slightly shorter than monospondylous centra. Diplospondyly begins above the anterior third or the middle of the pelvic base. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.55-0.62 (mean 0.59) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.06-1.20 (mean 1.13) in six specimens.

The smallest free-living specimen I have seen was 607 mm TL, while the largest embryo was 555 mm. Three mature males examined were 1,220, 1,235, and 1,322 mm TL, with clasper lengths equal to 7.3, 7.7, and 7.5% TL, respectively. Wheeler (1953, 1963), Fourmanoir (1961), and Bass et al. (1973) have reported extensively on this species, including its biology, variously under the names *amblyrhynchos*, *amblyrhynchus*, or *spallanzani*. Wheeler's accounts are of specimens mainly from the Mauritius-Seychelles area but also include some from Zanzibar or the East African coast, Fourmanoir's material was from off Madagascar, while that of Bass et al. included specimens from the St. Brandon area north of Mauritius, from off Madagascar, and from the Mozambique and northern Natal coasts. Some of their conclusions are in Table 57.

Table 57.—Number of embryos per litter, size at birth, size at maturity, and maximum size of *Carcharhinus wheeleri*.

	Wheeler (1953; 1963)	Fourmanoir (1961)	Bass et al. (1973)
No. of embryos per litter	Range (mean) 1-4 (2.4) <i>n</i> = 89	Range (mean) 2-4 (3.2) <i>n</i> = 4	Range (mean) 1-4 (2.7) <i>n</i> = 3
Total length when born	ca. 700 mm	500-670 mm	—
Total length at sexual maturity			
Female	1,250 mm	ca. 1,350	1,200 mm
Male	1,120-1,400 mm		1,210 mm
Maximum total length			
Female	1,720 mm		—
Male	1,680 mm	ca. 1,700 mm	—

Wheeler noted that males were sexually mature at lengths between 1,120 and 1,400 mm, while the smallest pregnant female he saw was 1,250 mm.

Distribution (see also Material examined).—Present records of this species are confined to the Red Sea and the western to central Indian Ocean. All of my material is from the Red Sea except for one specimen each from the Gulf of Aden, Kenya, and Réunion. Wheeler (1953, 1963) reported the species (as *amblyrhynchos* and *amblyrhynchus*) as abundant in the Mauritius-Seychelles area, and noted it was present at Zanzibar and the "East African coast." Fourmanoir (1961) recorded it (as *amblyrhynchus*) as common on the west and northwest coasts of Madagascar. D'Aubrey (1964) mentioned it (as *spallanzani*) as being recorded from Mozambique (Bazaruto Island) and from the northeast coast of South Africa (Sordwana Bay), while Bass et al. (1973) summarized the above records of its distribution.

Material examined.—Holotype: USNM 197418, mature male, 1,322 mm, Red Sea, 1962, E. Clark. Paratypes: MNHN 8001, female embryo, 521 mm, Indian Ocean, Réunion; BMNH 1925.7.20.7-8, female embryo, 539 mm, and male embryo, 555 mm, Gulf of Aden, A. Ehrenreich; MSNG C.E. 34564, male, 595 mm, Red Sea, Dissei Island, 1892, *Scilla*; NMV 61.441, three males, 607, 677, and 1,220 mm (the last mature), Red Sea, Hasani Island, 1895; USNM 197675, male, ca. 670 mm, Kenya, Tiwi, 19 December 1961, N. Mitton; ISZZ 10687, male, 720 mm, Red Sea, Koseir, C. B. Klunzinger; NMV 61-448, two females, 750 and 1,290 mm, and male, 757 mm, Red Sea, Ravaya, 1897; NMV (no number), male, 890 mm, Red Sea; NMV 61-446, female, 1,145 mm, Red Sea, Daedalus Rocks, 1897; NMV 61-431, female, 1,200 mm, Red Sea, Daedalus Rocks, 1897; SMF 4363, dried, mounted skin of mature male, 1,235 mm, Red Sea, Farasan Islands, Sarsa Island, 27 November 1957, W. Klausewitz.

Carcharhinus albigmarginatus (Rüppell, 1837)

Figures 53, 54

Carcharias albigmarginatus Rüppell, 1837:64, pl. 18, fig. 1. Several specimens were taken but no type material designated by Rüppell; Red Sea, Ras Mehamet. Klausewitz (1960:293) designated a lectotype.

Eulamia (Platypodon) platyrhynchus Gilbert, 1892:543-544. Several specimens obtained but no details are given of type material; Revillagigedo Islands (Clarion and Socorro), also one specimen from Magdalena Bay, Lower California. Rosenblatt and Baldwin (1958:151) designated a lectotype.

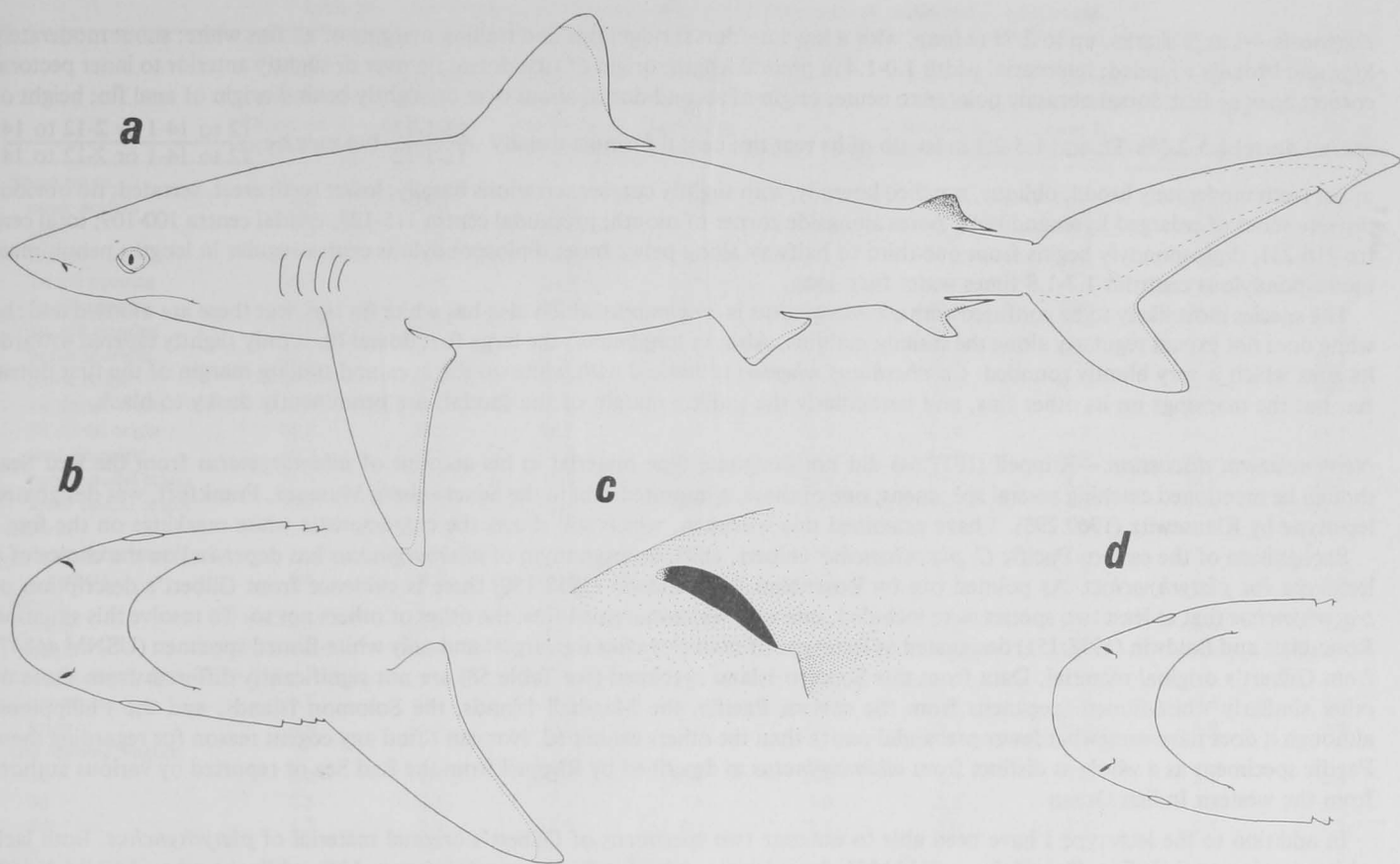


Figure 53.—*Carcharhinus albimarginatus*, UCLA 55-306, 1,066 mm TL, female from Cocos Island, Costa Rica: *a*, left side; *b*, underside of head; *c*, enlarged left nostril; *d*, underside of head of USNM 140963, 1,540 mm TL, female from Marshall Islands.

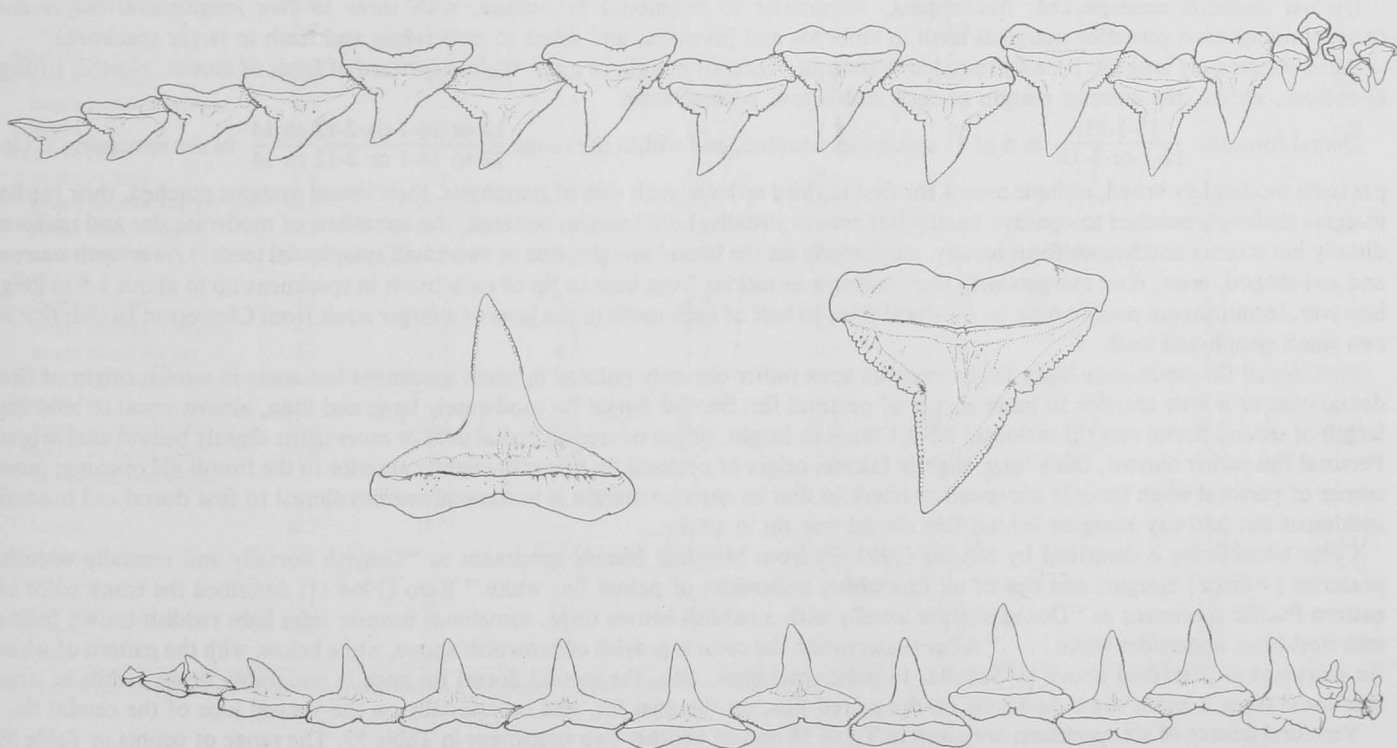


Figure 54.—*Carcharhinus albimarginatus*, UCLA 58-292, 2,157 mm TL, from eastern Pacific, Clipperton Island: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

Table 59.—Vertebral numbers in two specimens of *Carcharhinus albimarginatus*.

Specimens		Precaudal	Caudal	Total
UCLA 48-1	Mexico: Baja California	125	104	229
SU 13503	Galapagos Islands	122	109	231
Range (including counts from Table 58)		116-125	100-109	216-231

begins above anterior third to middle of pelvic base. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.55-0.60 (mean 0.58) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.04-1.15 (mean 1.09) in four specimens.

The smallest free-living specimen seen by me was 625 mm TL, and the largest embryo 683 mm. Of the few males seen, one of 1,825 mm was mature with a clasper length of 8.6% TL. Fourmanoir (1961), reporting on material from the west coast of Madagascar (measurements of 25 specimens and total lengths of another 68), stated that the size at birth ranges from 550 to 800 mm, that there are 6-8 in a litter, that maturity (of females?) is reached at more than 2,150 mm, and that maximum length is 3 m (though the largest specimen actually recorded by Fourmanoir was 2,750 mm). Measurements of clasper length given by Fourmanoir (1961, tables following p. 52) indicate that males of 1,840 mm TL are mature. Gohar and Mazhar (1964) described a male, 1,680 mm long, from the Red Sea as being mature with a clasper length of 9% TL. Wheeler's valuable accounts (1953, 1963) of 429 specimens from the Mauritius-Seychelles area (including measurements of 5, and data on reproduction for many others) agree well with my data and those of Fourmanoir; some of Wheeler's findings are that the number of embryos can range from 1 to 10, that males approach sexual maturity at 1,650-1,730 mm and are fully mature at 1,800 mm, and that maturity in both sexes is reached when the sharks are about 3 yr old. Bass et al. (1973) summarized the above data, as well as their own, for the western Indian Ocean. Their material included a litter of six embryos; their smallest mature male and female were 1,740 and 1,990 mm; and their largest specimens were 2,040 mm for male and 2,080 mm for female.

Distribution (see also Material examined).—Localities represented by specimens seen by me are: Red Sea, Philippine Islands, Solomon Islands, Marshall Islands, and the eastern Pacific including Baja California (Magdalena Bay) and the offshore islands southwards (Revillagigedo, Clipperton, Cocos, and Galapagos). Kato et al. (1967) reported *albimarginatus* from off Guatemala and Colombia, and Kato and Carvallo (1967) found it was common at the Revillagigedo Islands (Socorro and San Benedicto, but not at Roca Partida, 65 mi to the west of Socorro). Accounts of the species from the western Indian Ocean include those of Wheeler (1953, 1963) from the Mauritius-Seychelles area, Fourmanoir (1961) from Madagascar, and Smith (1957) from northern Mozambique; a more recent and detailed survey by Bass et al. (1973) incorporated these and other records, and gave *albimarginatus* a long coastal distribution from Tanganyika to northern Natal, and also reported it as common off Madagascar and many offshore islands and extending to as far east as Chagos Island. Martens (1876) reported it from the Strait of Makassar, Nakamura (1936) from Taiwan, and Bryan (1973) from Guam. Fourmanoir (see footnote 18) advised me that he has taken it off New Caledonia. Despite the above wide distribution in the Indian Ocean, western Pacific, and eastern Pacific, there is as yet no record of *albimarginatus* from Australia. Also it was not found in the extensive survey of the central Pacific (centered on the Hawaiian Islands) reported by Strasburg (1958) nor in that of the Hawaiian Islands by Tester (see footnote 4).

Material examined.—UCLA 48-1, male embryo, 310 mm, Mexico, Baja California, near Magdalena Bay, 7 September 1948; SIO 48-271, male embryo, 315 mm, Mexico, Baja California, near Magdalena Bay, 7 September 1948; UCLA 58-292, female embryo, 497 mm, Clipperton Island, 11 August 1958, W. Baldwin and party; SIO 60-122, female embryo, 532 mm, Mexico, Revillagigedo Islands, Socorro Island, 31 March 1960, H. R. MacMillan; SU 12578, female embryo, 625 mm, Mexico, Revillagigedo Islands, Clarion Island, R. E. Snodgrass and E. Heller; SU 13667, female embryo, 683 mm, Philippine Islands, Dumaguete, June 1931, A. W. Herre; USNM 196794, male, 702 mm, Revillagigedo Islands, Socorro Island, 20 January 1962; CNHM 41900, female, 715 mm, Costa Rica, Cocos Island, 22 February 1941, L. P. Woods; SU 13503, male, ca. 735 mm, Galapagos Islands, Albemarle Island, Tagus Cove, 9 January 1929, A. W. Herre; USNM 196793, male, 752 mm, Revillagigedo Islands, Socorro Island, 19 January 1962; UCLA 55-121, male, 775 mm, and female, 857 mm, Mexico, Revillagigedo Islands, San Benedicto Island, 14 April 1955; USNM 220997, female, 815 mm, Solomon Islands, New Georgia, 1944, W. M. Chapman; USNM 46847, female, 908 mm [lectotype of *Eulamia (Platypodon) platyrhynchus*], Mexico, Revillagigedo Islands, Socorro Island, 1889, *Albatross*; UCLA 53-51, female, 930 mm, Mexico, Revillagigedo Islands, Socorro Island, 18 March 1953, *Paolina T*; SMF 3582, dried and mounted, immature male, ca. 1,000 mm (lectotype of *Carcharias albimarginatus*), Red Sea, Ras Mehamet, 1834, E. Rüppell; UCLA 55-306, female, 1,066 mm, Costa Rica, Cocos Island, C. E. Blunt; NMV 61-442, female, 1,130 mm, Galapagos Islands, 1901, Jordan; USNM 140963, female, 1,540 mm, Marshall Islands, Eniwetok Atoll, 26 May 1946, L. P. Schultz and crew of *Bowditch*; USNM 197389, mature male, 1,825 mm, Revillagigedo Islands, Socorro Island, 3 August 1962, S. Kato; UCLA 58-292, jaws of adult, 2,157 mm, Clipperton Island, 17 August 1958, W. Baldwin and party; also SMNS 1641, jaws only, Red Sea, Koseir, 1869, Klunzinger.

Carcharhinus obscurus (Lesueur, 1818) Figures 55, 56

Squalus obscurus Lesueur, 1818:223-224, pl. 9. No type material mentioned, nor locality other than "North America" in title.

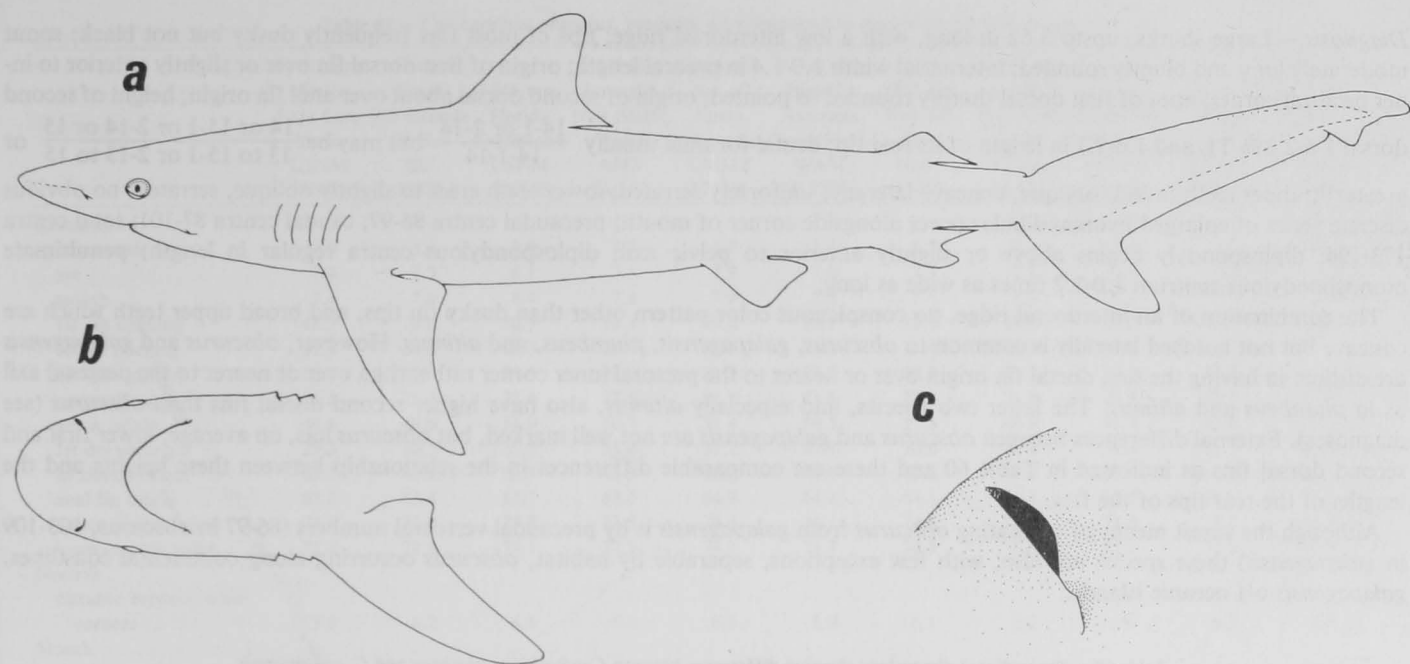


Figure 55.—*Carcharhinus obscurus*, UCLA 58-373, 961 mm TL, female from Baja California: a, left side; b, underside of head; c, enlarged left nostril.

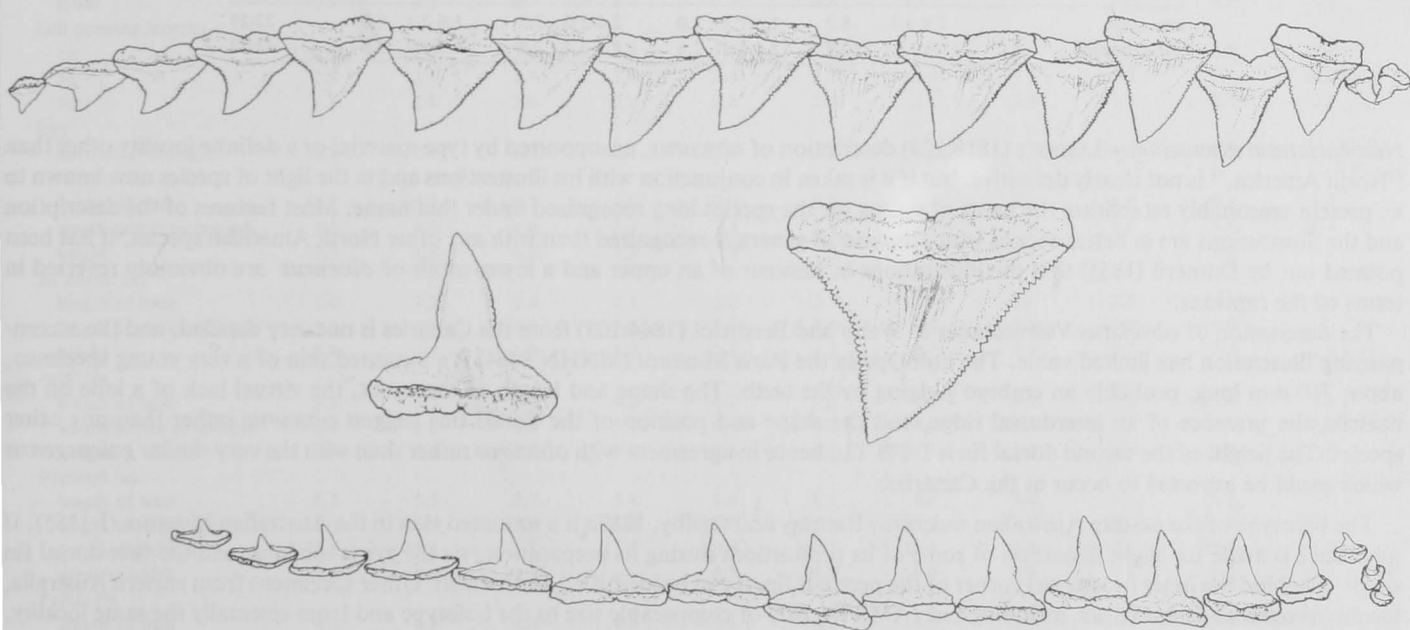


Figure 56.—*Carcharhinus obscurus*, UCLA 63-678-5A, 3,211 mm TL, male from California: right upper and lower teeth (symphysis to the right); inset teeth are fifth upper and lower teeth.

Carcharias (Prionodon) obvelatus Valenciennes in Webb and Berthelot, 1844:103-104, pl. 26. Holotype, female, 800 mm, Canary Islands.

Carcharias macrurus Ramsay and Ogilby, 1887a:163-164. Holotype, male, $34 \frac{2}{5}$ in (874 mm), Port Jackson, New South Wales, Australia; 1887b:1024. Correction of error in original description.

Galeolamna (Galeolamnoides) eblis Whitley, 1944:252-255, text fig. 1. Holotype, female, 950 mm, Western Australia, off Bald Head, towards Breaksea Island; "allotype," male, 1,375 mm, Western Australia, Pelsart Island in Houtmans Abrolhos; AMS card catalogue also list as paratype a female, 950 mm, Western Australia, off Bald Head; while Whitley cites as additional specimens a pair of jaws in the Fisheries Office, Geraldton, Western Australia, and a female, 935 mm, in the Western Australian Museum, both from Western Australia.

Carcharinus Iranzae Fourmanoir, 1961:40, pl. 13, fig. C, table on p. 69. No type material designated but measurements are given of three specimens of 2,270, 2,420, and 2,510 mm, and two others of 2,570 and 3,200 mm are mentioned; west coast of Madagascar.

Diagnosis.—Large sharks, up to 3.62 m long, with a low interdorsal ridge; tips of most fins frequently dusky but not black; snout moderately long and bluntly rounded; internarial width 1.0-1.4 in preoral length; origin of first dorsal fin over or slightly anterior to inner pectoral corner; apex of first dorsal sharply rounded to pointed; origin of second dorsal about over anal fin origin; height of second dorsal 1.5-2.3% TL and 1.6-2.1 in length of its rear tip; dental formula usually $\frac{14-1 \text{ or } 2-14}{14-1-14}$ but may be $\frac{14 \text{ or } 15-1 \text{ or } 2-14 \text{ or } 15}{13 \text{ to } 15-1 \text{ or } 2-13 \text{ to } 15}$ or greater²⁰; upper teeth broad, oblique, concave laterally, uniformly serrated; lower teeth erect to slightly oblique, serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 86-97; caudal centra 87-101; total centra 173-194; diplospondyly begins above or slightly anterior to pelvic axil; diplospondylous centra regular in length; penultimate monospondylous centrum 1.0-1.2 times as wide as long.

The combination of an interdorsal ridge, no conspicuous color pattern other than dusky fin tips, and broad upper teeth which are concave but not notched laterally is common to *obscurus*, *galapagensis*, *plumbeus*, and *altimus*. However, *obscurus* and *galapagensis* are distinct in having the first dorsal fin origin over or nearer to the pectoral inner corner rather than over or nearer to the pectoral axil as in *plumbeus* and *altimus*. The latter two species, and especially *altimus*, also have higher second dorsal fins than *obscurus* (see diagnoses). External differences between *obscurus* and *galapagensis* are not well marked, but *obscurus* has, on average, lower first and second dorsal fins as indicated in Table 60 and there are comparable differences in the relationship between these heights and the lengths of the rear tips of the fins.

Although the surest means of separating *obscurus* from *galapagensis* is by precaudal vertebral numbers (86-97 in *obscurus*, 103-109 in *galapagensis*) these species are also, with few exceptions, separable by habitat, *obscurus* occurring along continental coastlines, *galapagensis* off oceanic islands.

Table 60.—Proportional dimensions showing differences between *Carcharhinus obscurus* and *C. galapagensis*.

Species	1st dorsal height as % TL		2d dorsal height as % TL		1st dorsal height 1st dorsal rear tip		2d dorsal height 2d dorsal rear tip		n
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
<i>obscurus</i>	5.8-9.9	8.2	1.5-2.3	2.0	2.0-3.0	2.5	1.6-2.1	1.9	22-27
<i>galapagensis</i>	9.1-12.1	10.7	2.1-3.3	2.6	2.5-3.4	2.9	1.3-1.7	1.6	25-32

Nomenclatural discussion.—Lesueur's (1818:223) description of *obscurus*, unsupported by type material or a definite locality other than "North America," is not clearly definitive, but if it is taken in conjunction with his illustrations and in the light of species now known to be present reasonably establishes the name *obscurus* for the species long recognized under that name. Most features of the description and the illustrations are in better accord with *obscurus* as generally recognized than with any other North American species. It has been pointed out by Duméril (1865) that the illustrations in Lesueur of an upper and a lower tooth of *obscurus* are obviously reversed in terms of the captions.

The description of *obvelatus* Valenciennes in Webb and Berthelot (1844:103) from the Canaries is not very detailed, and the accompanying illustration has limited value. The holotype in the Paris Museum (MNHN 3464) is a mounted skin of a very young specimen, about 760 mm long, probably an embryo judging by the teeth. The shape and length of the snout, the virtual lack of a lobe on the nostrils, the presence of an interdorsal ridge, and the shape and position of the dorsal fins suggest *obscurus* rather than any other species. The height of the second dorsal fin is 1.8% TL, hence in agreement with *obscurus* rather than with the very similar *galapagensis* which could be expected to occur at the Canaries.

The holotype of the eastern Australian *macrurus* Ramsay and Ogilby, 1887a is a mounted skin in the Australian Museum (I.1155). If allowance is made for slight distortion of some of its proportions during its preparation, viz the eye is too large and the first dorsal fin origin is behind the inner (posterior) corner of the pectoral fin, it can be identified as *obscurus*. Other specimens from eastern Australia, locally recognized as *macrurus*, including one (AMS IA.167) of comparable size to the holotype and from essentially the same locality, which was illustrated by McCulloch (1921:457, pl. 37), show no disagreement with *obscurus* in proportions, form, and vertebral count and confirm the view that *macrurus* is conspecific with *obscurus*.

The holotype, "allotype," and paratype of the western Australian *eblis* Whitley, 1944 in the Australian Museum are all fragmentary, comprising only jaws, teeth, and small pieces of skin. The holotype jaws and teeth resemble those of *obscurus* and have an appropriate dental formula of $\frac{14-2-14}{14-1-14}$. The vertebral count of the allotype (see p. 125) given by Whitley (1944:255) conforms to *obscurus*, as do the illustrations of the same specimen—the only one figured. The measurements given by Whitley for the holotype and allotype show no significant differences from *obscurus* other than in the snout length which is slightly longer, but I believe this may be due to differences in taking the measurements, for another Western Australian specimen (WAM. P.7199) referable to *eblis* and measured by me (see Table 61) does not show this difference. Whitley himself (1944:255) noted that *eblis* is "most closely allied to *macrurus* (Ramsay and Ogilby) from New South Wales, but the incomplete interdorsal ridge is again diagnostic; it is always complete in *macrurus*." This last statement is not borne out by examination of the holotype of *macrurus* in which the middorsal ridge, as in other specimens of *obscurus*, "does not completely unite the two dorsal fins."

A pair of jaws (WAM. P.6667) in the Western Australian Museum, from a female of 935 mm which Whitley cited as an additional specimen to the type series of *eblis*, has a dental formula of $\frac{16-2-16}{15-1-14}$ and seems identifiable as *brachyurus*.

²⁰Bass et al. (1973) showed that occasionally there may be as many as 16 lateral teeth in the upper and lower jaws.

Table 61.—*Carcharhinus obscurus*, proportional dimensions in percentage of total length.

	♂ 812 mm Mexico Baja Cali- fornia USNM 46850	♂ 834 mm Brazil Rio Grande do Sul SU 52870	♂ 863 mm Florida Englewood USNM 106546	♀ 866 mm Australia New South Wales AMS 1A.167	♂ 915 mm Sea of Japan Hamada UMMZ 179016	♂ 948 mm Western Australia North Perth WAM P.7199	♀ 957 mm Red Sea Suez NMV 61459	♀ 961 mm Mexico Baja Cali- fornia UCLA 58-373	♀ 1,260 mm New Jersey USNM 196666	♂ 1,456 mm South Africa Algoa Bay USNM 197674	♀ 3,200 Florida Sarasota
Snout tip to											
outer nostrils	3.9	3.6	3.9	3.7	3.7	3.4	3.5	4.1	3.4	3.4	2.6
eye	7.4	7.5	8.1	7.5	7.9	7.0	7.3	7.7	6.9	7.2	5.9
mouth	7.4	7.9	8.4	7.8	7.9	7.5	7.5	7.9	7.3	7.5	5.9
1st gill opening	18.7	18.0	20.3	18.3	19.2	18.7	18.5	18.8	17.9	19.2	18.2
3d gill opening	21.1	20.5	22.3	21.4	21.5	21.4	21.4	21.3	21.5	21.7	21.7
5th gill opening	22.9	22.2	24.0	23.6	23.3	23.2	23.3	23.1	22.3	23.3	23.9
pectoral origin	22.2	21.3	22.6	22.6	21.7	21.6	22.4	21.8	20.9	22.7	22.7
pelvic origin	49.6	49.6	51.0	50.7	51.4	50.5	51.5	48.9	51.3	49.6	53.6
1st dorsal origin	29.3	30.5	31.5	31.6	31.2	31.7	30.6	30.9	31.4	31.1	32.9
2d dorsal origin	63.3	63.2	63.7	63.3	65.0	64.6	63.2	61.6	63.7	63.1	65.8
anal fin origin	62.8	63.4	62.7	62.5	64.7	64.2	63.5	61.1	63.5	63.1	65.3
upper caudal origin	73.0	73.0	73.8	73.7	74.4	74.1	74.8	72.9	73.3	73.2	75.8
lower caudal origin	72.8	72.4	73.1	72.5	74.1	73.7	74.5	71.8	72.7	72.6	75.0
Nostrils											
distance between inner corners	5.8	6.2	6.1	6.0	6.3	5.9	6.1	6.0	6.0	6.2	6.1
Mouth											
width	7.1	8.9	8.1	7.3	8.0	7.4	7.6	7.6	8.9	8.4	10.1
length	4.6	4.4	4.6	4.5	4.4	4.4	4.5	4.3	4.0	4.5	3.6
Labial furrow lengths											
upper	0.9	0.4	0.7	0.3	0.5	0.4	0.3	0.4	0.3	0.4	0.6
lower	0.9	0.5	0.7	0.4	0.7	0.4	0.5	0.5	0.6	0.7	0.5
Gill opening lengths											
1st	2.1	2.6	3.0	2.4	2.9	2.6	2.6	2.9	3.2	3.6	3.3
3d	2.7	3.1	3.7	3.0	3.6	3.1	2.9	3.1	3.7	3.6	4.0
5th	2.1	2.4	2.6	2.4	2.6	2.4	2.1	2.1	2.5	2.7	2.7
Eye											
horizontal diameter	1.8	2.1	2.0	2.1	2.0	1.9	1.8	1.7	1.5	1.8	1.0
1st dorsal fin											
length of base	11.7	10.2	9.7	9.5	10.0	8.9	9.7	9.1	9.0	9.8	9.7
length posterior margin	3.3	3.0	3.0	3.3	3.3	2.9	3.2	3.3	3.6	3.5	3.4
height	7.5	6.8	6.0	7.3	7.8	7.5	7.7	8.1	9.7	9.0	9.1
2d dorsal fin											
length of base	2.6	3.2	3.4	3.1	3.0	2.5	3.8	3.6	3.6	3.1	4.2
length posterior margin	3.3	3.6	3.4	3.6	3.9	3.5	3.6	3.9	3.7	4.0	—
height	1.8	2.0	1.9	1.8	2.1	1.8	2.1	1.9	2.3	2.2	2.1 +
Anal fin											
length of base	3.9	3.5	4.2	4.2	4.2	3.5	4.2	4.6	3.6	3.8	4.6
length posterior margin	2.8	3.2	3.0	3.5	3.4	3.2	3.4	3.4	3.5	3.8	3.2
height	2.6	2.6	2.7	2.4	2.6	2.5	2.7	2.8	2.9	3.2	3.8
Pectoral fin											
length of base	5.5	5.5	5.7	5.4	5.4	6.1	5.6	5.4	6.3	6.1	7.0
length anterior margin	18.0	16.9	17.6	16.8	17.8	17.2	17.6	17.7	19.4	18.8	21.6
length distal margin	12.2	10.3	11.2	11.5	13.6	12.1	12.5	13.0	15.7	15.3	18.8
greatest width	8.5	8.3	8.3	—	8.5	8.0	8.0	8.8	9.8	9.7	—
Pelvic fin											
length of base	4.4	4.5	4.4	4.6	5.1	4.2	4.5	4.9	4.7	5.4	5.8
length anterior margin	5.3	4.8	4.8	4.8	4.7	4.8	4.6	5.4	5.5	5.5	5.4
length distal margin	4.4	4.9	4.8	4.3	5.2	4.5	4.6	4.8	5.2	5.9	6.3
length of claspers	—	2.6	2.8	—	2.2	2.2	—	—	—	2.5	—
Caudal fin											
length of upper lobe	26.1	26.6	26.7	26.8	26.1	26.7	26.2	27.1	26.7	27.5	25.8
length of lower lobe	10.8	11.0	10.9	11.5	11.6	11.6	11.3	11.9	12.4	12.0	11.8
Trunk at pectoral origin											
width	11.1	12.8	13.1	11.5	11.5	11.5	10.7	11.6	12.5	12.5	14.4
height	9.6	10.5	—	10.6	12.3	11.1	10.8	11.0	10.7	11.4	14.7
Dental formula	—	15-2- ? 14-1-14	—	—	14-2-14 14-1-14	14-1-14 14-1-14	14-1-14 13-1-13	14-1-14 15-1-15	14-1-14 7-7-7	15-2-15 14-1-14	15-2-15 14-2-14
Vertebrae											
precaudal	88	92	92	90	90	91	—	90	93	91	89
caudal	96	95	98	—	94	97	—	90	101	97	97
total	184	187	190	—	184	188	—	180	194	188	186

¹Syntype of *Eulamia (Platypodon) platyrhynchus*.

Fourmanoir's (1961:40) account of *iranzae* from the west coast of Madagascar is brief, and comparison is made with *leucas* though the author suggested that *iranzae* showed more resemblance to *obscurus* which is also reported (on p. 76). Recognition of *iranzae* as *obscurus* is not possible from this account, and no type material appears to have been deposited. However, in a later paper Fourmanoir (1964:57) synonymized *iranzae* with *obscurus* and reported on additional specimens. The new data provided, including first dorsal fin heights, confirm that the species is *obscurus*.

Duméril (1865:372) pointed out that the type material of *henlei* Valenciennes in Müller and Henle, 1841 from Cayenne includes two specimens. Elsewhere in this account (p. 71) I refer two of the three type specimens to *porosus* and designate one of these two as a lectotype of *henlei*. The third specimen, a mounted skin (A.9657) in the Paris Museum is in very poor condition, having lost its caudal and anal fins, but my impression from examining it is that it agrees better with *obscurus* than with any other species. This specimen was identified by Bertin (1939:72) as *melanopterus* but such identification must be discounted.

The original material of *platyrhynchus* Gilbert, 1892 from the eastern Pacific included three species (see p. 118 of this account) of which one, represented by USNM 46850 from Magdalena Bay, can be identified as *obscurus* (see Table 61). Rosenblatt and Baldwin's (1958:151) selection of a lectotype for *platyrhynchus* (here synonymized with *albimarginatus*) removed the Magdalena Bay specimen from consideration under that name.

Although *obscurus* is now known to be present in the eastern Pacific, it has not, until very recently (Kato et al. 1967) been identified by that name but instead, for the most part and particularly in substantive accounts such as Rosenblatt and Baldwin (1958) and Kato (1964), has been referred to *lamiella* Jordan and Gilbert, 1883b. This referral is incorrect for as shown here (p. 174) the holotype of *lamiella* is identifiable as *brachyurus* Günther, 1870. In Jordan and Gilbert's account of *lamiella* they mentioned, in addition to the holotype, a pair of jaws from a large specimen off lower California—these jaws were said to have considerably broader teeth than those of the juvenile holotype, and hence would be unlike adult *brachyurus* but would resemble *obscurus*. I have not been able to locate these jaws but it is conceivable that they were from an *obscurus* and that it was *obscurus* that Jordan and Gilbert had in mind when describing *lamiella*. Be this as it may, the designated holotype of *lamiella* is *brachyurus*, hence *lamiella* must be synonymized under that name.

Description (see also Table 61).—Large sharks, growing to at least 3.6 m TL. Midline of back between dorsal fins with a low dermal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles close-packed, overlapping, subcircular in outline in small specimens, more nearly rhomboid in larger, each with three longitudinal ridges and three rather strong posterior marginal teeth in small specimens, but with five to seven ridges in larger specimens and up to five posterior teeth.

Snout moderately long, bluntly rounded in contour. Anterior margin of eye is above or slightly forward of front of mouth. Nostrils strongly oblique, slitlike, the anterior margin of each with a low, pointed lobe.

Dental formula $\frac{14-1 \text{ or } 2-14}{14-1 \text{ or } 2-14}$ in 8 of 24 specimens counted; $\frac{15-1 \text{ or } 2-15}{14-1 \text{ or } 2-14}$ in 7; $\frac{14 \text{ or } 15-1 \text{ or } 2-14 \text{ or } 15}{14 \text{ or } 15-1 \text{ or } 2-14 \text{ or } 15}$ in 5; and $\frac{14-1 \text{ or } 2-14}{13-1 \text{ or } 2-13}$ in

4. Upper teeth broad, oblique except for the first one or two series on each side of symphysis, their lateral margins concave, their medial margins weakly concave basally but convex distally, both margins coarsely serrated, the serrations of uniform size; one or two small symphyseal teeth. Lower teeth narrow, sometimes slightly expanded distally in large specimens (as figured here, Fig. 56), erect or at most slightly oblique, both margins concave to notched basally, uniformly, and finely serrated; one, or occasionally two, small symphyseal teeth.

First dorsal fin moderately low, its apex tending to be rounded, its anterior margin moderately to strongly convex; origin of first dorsal fin usually above inner (posterior) corner of pectoral fin but sometimes slightly anterior though never farther forward than the posterior third of the inner (posterior) margin of pectoral. Second dorsal fin moderately low and long, distinctly smaller than anal fin, its distal margin almost straight or at most weakly concave; length of second dorsal rear tip 1.6-2.1 (mean 1.9) times second dorsal height; origin of second dorsal about over anal fin origin. Pectoral fins moderately long, slender, pointed; origin of pectorals below the level of the fourth gill openings or below and between the levels of the third and fourth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches at least to first dorsal axil and usually farther back, to about halfway along the first dorsal rear tip in small specimens but to just behind the tip in large specimens.

Color in life was described by Kato (1964, as *lamiella*) as "Dorsal surface brownish-gray to dark gray; undersides white." After preservation in alcohol the color is essentially the same although some specimens I have seen have had a streak of faintly paler color extending forward along the flank from above the pelvic base to about the first dorsal axil, cutting off a similar streak of darker color below it; also several specimens have had dusky-tipped or dusky-margined fins, particularly the pectoral, second dorsal, and caudal fins.

Vertebral counts of 10 specimens are given in Table 61 and of another 10 specimens in Table 62. Bass et al. (1973) recorded precaudal counts of 87-97 (mean 91.1) and total counts of 175-191 from 99 specimens from the east coast of southern Africa.

Centrum diameter noticeably greater than centrum length except for last few monospondylous centra at posterior of abdomen which are about square or even slightly longer than wide. Diplospondylous centrum length regular. Diplospondyly begins above axil of pelvic fin or slightly anterior to axil but not farther forward than the posterior third of pelvic base. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.85-1.00 (mean 0.95) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.24-1.81 (mean 1.57) in 15 specimens.

The smallest, apparently free-living specimen I have seen was 855 mm TL, while the largest embryo was 863 mm. Springer (1938) noted embryos of 950-965 mm in late January off Englewood, Fla., while later (1960) he presented information that embryos are born at about 39 in (1,000 mm). Comparable data are provided by: Bigelow and Schroeder (1948) who suggested that birth size is usually about 965 mm in Atlantic specimens; D'Aubrey (1964) who noted birth size at about 900 mm in South African material; Clark and von

Table 62.—Vertebral numbers in 10 specimens of *Carcharhinus obscurus*.

Specimens		Precaudal	Caudal	Total
SU 52850	Brazil	93	100	193
USNM 198163	Uruguay	93	97	190
USNM 198163	Uruguay	92	92 +	184 +
USNM 198163	Uruguay	94	—	—
UCLA 60-15	Mexico, Baja Cali- fornia	86	91	177
SU 11592	Mexico, Mazatlan	86	87	173
BMNH 1960.1.5.5	Japan	89	96	185
AMS IB.1377	Australia, New South Wales	91	94	185
QMB 1.7976	Australia, Queens- land	92	98	190
AMS IB.1609	Western Australia	87	87	174
Range (including counts from Table 61)		86-94	87-101	173-194

¹"Allotype" of *Galeolamna (Galeolamnoides) eblis*. Count from Whitley (1944).

Schmidt (1965) who reported on a litter of seven embryos, 840-940 mm long, born at Cape Haze Marine Laboratory, Fla., in late December, and who noted that the largest embryos they found were 1,000 mm long; and Bass et al. (1973) who found that size at birth could range from 690 to 1,000 mm but was usually between 800 and 900 mm in their very extensive sample from the east coast of southern Africa. Clark and von Schmidt (1965) also gave data on 18 gravid females from Florida, of which 14 taken during winter months had embryos 430-700 mm long while the remaining four taken at the same time of year had embryos of 850-1,000 mm; they remarked that Springer's (1938) record of *obscurus* embryo sizes showed a comparable division into two distinct size groups and suggested that the gestation period may be 16 mo. Fourmanoir (1964) observed that one female from Madagascar taken in June had embryos 525 mm long while another taken at the same time contained only eggs, and suggested that reproduction must extend over a long period. Bass et al. (1973) found no clear indication of seasonality in reproduction from their data for southern Africa, but there was an increase in the number of births from April to June.

The number of embryos per litter has been recorded as 6-10 (mean 7.7) in 16 litters by Clark and von Schmidt (1965); as 9-12 (mean 10) by D'Aubrey (1964); as 6-14 (mean 9.9) in 14 litters by Bass et al. (1973); and as 10 for one litter each by Springer (1938) and Fourmanoir (1964).

Of the few males that I have measured, all were juvenile or half grown, the largest 1,456 mm, and all immature with clasper lengths ranging from 2.1 to 2.8% TL. Evidence on the size at which maturity is reached in the male is rather scanty. Clark and von Schmidt (1965) recorded only two males, both mature, 2,990 and 3,160 mm long with clasper lengths of 8.1 and 8.9% TL, from their Florida material. Springer (1960) gave data on "adult" males, presumably mature, over a size range of about 2,790-3,370 mm from the western Atlantic. Bass et al. (1973) provided more extensive data from southern Africa, which indicate that males mature at about 2,800 mm. They also reported that females are mature at lengths of 2,600-3,000 mm. The smallest gravid female recorded by Clark and von Schmidt (1965) was 2,890 mm. The maximum length recorded for *obscurus* is about 3,625 mm (Springer 1960) for a female; the same author indicated that males reach about 3,370 mm. These lengths are in close accord with Bass et al.'s (1973) findings of 3,570 and 3,240 mm for females and males from southern Africa.

Distribution (see also Material examined).—The distribution of *obscurus* from literature accounts includes both sides of the Atlantic, the northeastern Pacific, and the western Indian Ocean. This general distribution is confirmed here and extended to Australia and Japan, but records of *obscurus* from oceanic islands cannot, for the most part, be substantiated. *Carcharhinus obscurus* seems to be, essentially, a species occurring along continental coastlines in the tropics and temperate regions. The detailed range given below is based for the most part on specimens I have examined, supplemented by data from De Kay (1842), Firth (1931), Cadenat (1937, 1950), Springer (1938, 1960), Fourmanoir (1961 as *iranzae*, 1964), Lowe (McConnell) (1962), Tibbo and McKenzie (1963), D'Aubrey (1964), Clark and von Schmidt (1965), Kato et al. (1967), Guitart Manday (1968), and Bass et al. (1973).

Western Atlantic from as far north as Georges Bank (lat. 41°20'N) and southwards including Massachusetts, New York, New Jersey, Florida (both coasts), Cuba [according to Guitart Manday (1968)], the Gulf of Mexico (off mouth of Mississippi, and off Nicaragua and Costa Rica), British Guiana, Cayenne, and Brazil (Vitória at middle coast of Brazil and Rio Grande do Sul in the south); eastern Atlantic from the Canary Islands in the north and southwards at Sénégal and off Capetown; Red Sea and western Indian Ocean from Suez, the west coast of Madagascar, and the east coast of Africa southwards to the tip of South Africa at lat. 34°37'S [this and numerous other records, including a comprehensive literature, are given in Bass et al. (1973) who, in addition, provided an admirable and detailed account of the life history and migratory patterns of *obscurus* off southeast Africa]; both west and east coasts of Australia, from Houtmans Abrolhos, Perth, and Bald Head in Western Australia, from Moreton Bay in Queensland, and from Botany Bay in New South Wales; Japan at Hamada and Nagasaki; and in the eastern North Pacific from San Diego and southwards to the Gulf of California, and occasionally at the Revillagigedo Islands (Kato et al. 1967).

Specimens identified as *obscurus* by Günther (1880) from Ascension and Bermuda, and by the same author (1870) from St. Helena, have been examined by me in the British Museum and proved to be *C. galapagensis*, thereby making suspect Günther's (1870) recognition of *obscurus* from Madeira. This failure to distinguish *obscurus* from the very similar *galapagensis*, coupled with the knowledge that *galapagensis* is found principally off oceanic islands (see p. 131), means that doubt must also be cast on the reports of *obscurus*

from Bermuda by Beebe and Tee-Van (1933) from the Bahamas by Springer (1960), and from off San Juan, Puerto Rico, by Backus (1957). However, the evidence is far from conclusive that *obscurus* is restricted to continental coastlines—in this account I identify as *obscurus* the type of *obvelatus* from the Canaries, as well as specimens from Japan—but in general this appears to be the essential nature of the distribution of the species. Certainly this view is in accord with earlier statements on the distribution of *obscurus* (as *lamiella*) in the eastern Pacific by Beebe and Tee-Van (1941) and Rosenblatt and Baldwin (1958).

The presence of *obscurus* in the eastern North Atlantic is not at all well documented other than for Cadenat's (1937, 1950) records, and the Canaries specimen (as *obvelatus*). Günther (1889) reported it, by name only, from Sierra Leone. Poll's (1951) account of trawling off the west coast of Africa from just south of the Equator to lat. 22°30'S did not record *obscurus*.

There is no firm evidence that *obscurus* occurs in the Mediterranean. Bigelow and Schroeder (1948) identified it from Spain on the basis of Rey's (1928) account of *commersonii*, and Tortonese (1950, 1951b) followed this proposal. However, the shark illustrated by Rey has a second dorsal fin that is too high for *obscurus* but suggests, instead, *galapagensis*.

Whitley's (1937) record of *macrurus* (= *obscurus*) from the Middleton and Elizabeth Reefs (north of Lord Howe Island to the east of Australia) does not appear ascribable to *obscurus* judging by the measurements he gave of one specimen in which the second dorsal height is 2.5% TL, but instead is more likely to be *galapagensis* which I recorded (p. 131) from Lord Howe Island.

Gohar and Mazhar (1964) reported *obscurus* from the Red Sea but their specimen, with tips and margins of all fins white, does not seem to be *obscurus*, even though the latter is present in the Red Sea.

Material examined.—BMNH 1960.1.5.5, male embryo, 530 mm, Japan, Choshi, March 1939, Shibayama Laboratory; SU 11592, male embryo, ca. 600 mm, Mexico, Mazatlan, 1895, Hopkins Expedition; ISZZ 8689, female, ca. 670 mm, Massachusetts, Woods Hole, Smithsonian Institution; ISZZ 8687, male, 700 mm, North America, Smithsonian Institution; QMB I.7976, female embryo, 705 mm, Australia, Queensland, Moreton Bay, July 1954, B. Dyer; ISZZ 8688, male, ca. 710 mm, Massachusetts, Woods Hole, Smithsonian Institution; USNM 187781, two embryos, female, 720 mm, and male, 730 mm, off Florida, 29°44'N, 80°18'W, 4 October 1960, *Silver Bay*; QMB I.7977, embryo, ca. 725 mm, Australia, Queensland, Moreton Bay, July 1954, B. Dyer; MNHN 3464, mounted skin of female, ca. 760 mm (holotype of *Prionodon obvelatus*), Canaries, Webb and Berthelot; SU 52850, male embryo, 771 mm, Brazil, Espírito Santo, Vitória, 28 August 1944; USNM 187782, four embryos, three males, 780–810 mm, and female, 810 mm, off Florida, 29°44'N, 80°18'W, 4 October 1960, *Silver Bay*; USNM 187780, two embryos, male, 800 mm, and female, 805 mm, off Florida, 29°44'N, 80°18'W, 4 October 1960, *Silver Bay*; USNM 46850, female, 812 mm [originally a syntype of *Eulamia (Platypodon) platyrhynchus*], Mexico, Baja California, Magdalena Bay; SU 52870, male embryo, 834 mm, Brazil, Rio Grande do Sul, Portal da Barra, 23 January 1945; UCLA 58-372, female, 855 mm, Mexico, Baja California, Black Warrior Lagoon, 1958; USNM 106546, male embryo, 863 mm, Florida, Englewood, off Stump Pass, 31 January 1938, Bass Biological Laboratory; AMS IA.167, female, 866 mm ("plesiotype" of *Carcharias macrurus*), Australia, Botany Bay, February 1921, J. H. Wright; AMS I.1155, mounted skin of male, 885 mm (holotype of *Carcharias macrurus*), Australia, New South Wales, Port Jackson; UCLA 49-393, female, 912 mm, Mexico, Baja California, Bahia Sebastian Viscaíno, September 1949, *Yellowfin*; UMMZ 179016, male, 915 mm, Sea of Japan, 3 or 4 mi off Hamada, 26 July 1929, C. L. Hubbs and K. Sakamoto; USNM 51290, female, ca. 920 mm, Japan, Nagasaki, D. S. Jordan and J. O. Snyder; MCZ 696, female, 928 mm, Mexico, Baja California, Magdalena Bay, Hassler Expedition; WAM P.7199, male, 948 mm, Western Australia, North Perth, Marmion Beach, 3 May 1964, S. Mattys; AMS IB.1615, jaws and skin fragments of female, 950 mm [holotype of *Galeolamna (Galeolamnoides) eblis*], Western Australia, off Bald Head, towards Breaksea Island, 30 September 1943; AMS IB.1616, teeth and skin fragments of male, 950 mm [paratype of *Galeolamna (Galeolamnoides) eblis*], Western Australia, off Bald Head, 5 October 1943; BMNH 1908.5.28.8, male, 955 mm, Cape of Good Hope, Gerrard; NMV 61-459, female, 957 mm, Suez; UCLA 58-373, two females, 961 and 1,005 mm, Mexico, Baja California, Guadalupe Island, 1958; UCLA 51-264, male, 1,040 mm, Mexico, Baja California, entrance to Santa Maria Bay, 12 October 1951; UCLA 60-51, male, 1,047 mm, Mexico, Baja California, Bahia Las Animas, 25-26 January 1960; USNM 196523, male, ca. 1,100 mm, off New Jersey, 39°45'N, 73°55'W, 25 August 1961, V. G. Springer; USNM 39990, male, partly skinned out, ca. 1,160 mm, Australia, New South Wales, Port Jackson, Australian Museum; AMS IB.1377, female, 1,175 mm, Australia, New South Wales, 22 January 1945, Hugh Ward; MNHN A9657, mounted skin (tail and anal fin missing) of female, ca. 1,200 mm (920 mm excluding tail) [syntype of *Carcharias (Prionodon) henlei* Valenciennes], Cayenne, Frère; USNM 196666, female, 1,260 mm, off New Jersey, 39°41'N, 73°48'W, 25 August 1961, V. G. Springer; AMS IB.1609, jaws and skin fragments of male, 1,375 mm ["allotype" of *Galeolamna (Galeolamnoides) eblis*], Western Australia, Houtmans Abrolhos, Pelsart Island, 5 November 1943; USNM 197674, jaws and tail of male, 1,456 mm, South Africa, Algoa Bay, off Port Elizabeth, 2 May 1963; QMB I.8252, jaws and cast of specimen, ca. 2,700 mm, Australia, Queensland; FSBC-VGS 60-100(1), jaws, some fins, and photograph of female, 3,100 mm, Florida, Pinellas County, Lower Boca Ciega Bay, 24 December 1960, V. G. Springer; female, 3,200 mm (discarded), Florida, Sarasota, 1½ mi off Cape Haze Marine Laboratory, 20 November 1963; SIO 63-678-5A, jaws and photographs of mature male, 3,211 mm, California, La Jolla, 28 July 1963; FSBC-VGS 60-100(2), jaws of female, 3,300 mm, Florida, Pinellas County, St. Petersburg Beach, 25 December 1960, A. McErlean.

Also USNM 197666, jaws of large specimen from South Africa, Algoa Bay, 2 May 1963; also jaws of many specimens at several institutions but in particular at DIRU, ORID, SAMC, and IFAN.

Carcharhinus galapagensis (Snodgrass and Heller, 1905)
Figures 57, 58, 59

Carcharias galapagensis Snodgrass and Heller, 1905:343-344. Holotype, embryo, 650 mm, Galapagos Is.; paratypes, ca. 500, 590, and 685 mm, Galapagos Is.; also dimensions of another specimen 550 mm long from the same locality.

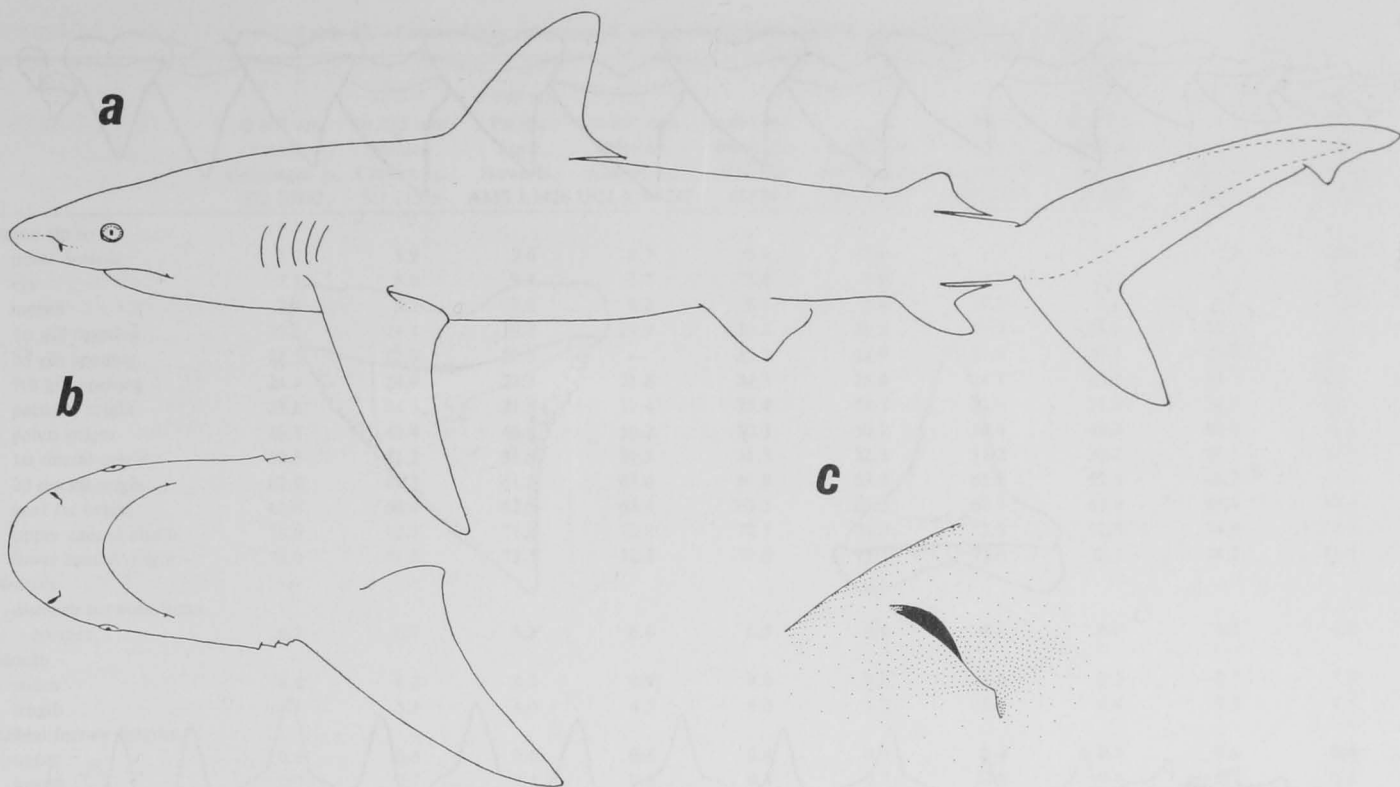


Figure 57.—*Carcharhinus galapagensis*, USNM 197390, 1,572 mm TL, female from Revillagigedo Islands: *a*, left side (rear tip of second dorsal reconstructed); *b*, underside of head; *c*, enlarged left nostril.

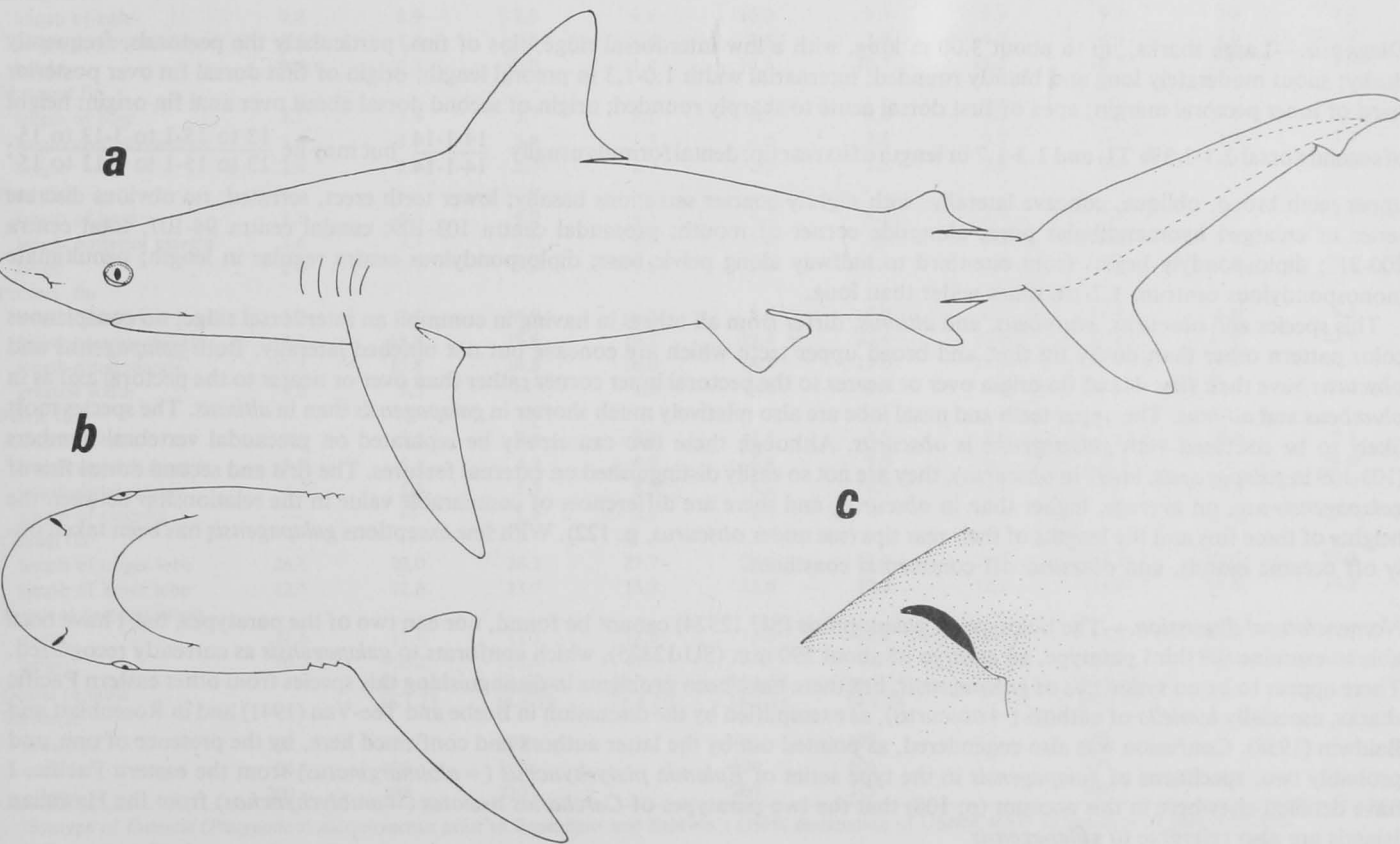


Figure 58.—*Carcharhinus galapagensis*, SU 12790, paratype of *Carcharias nesiotes*, 982 mm TL, female from Hawaiian Islands: *a*, left side; *b*, underside of head; *c*, enlarged left nostril.

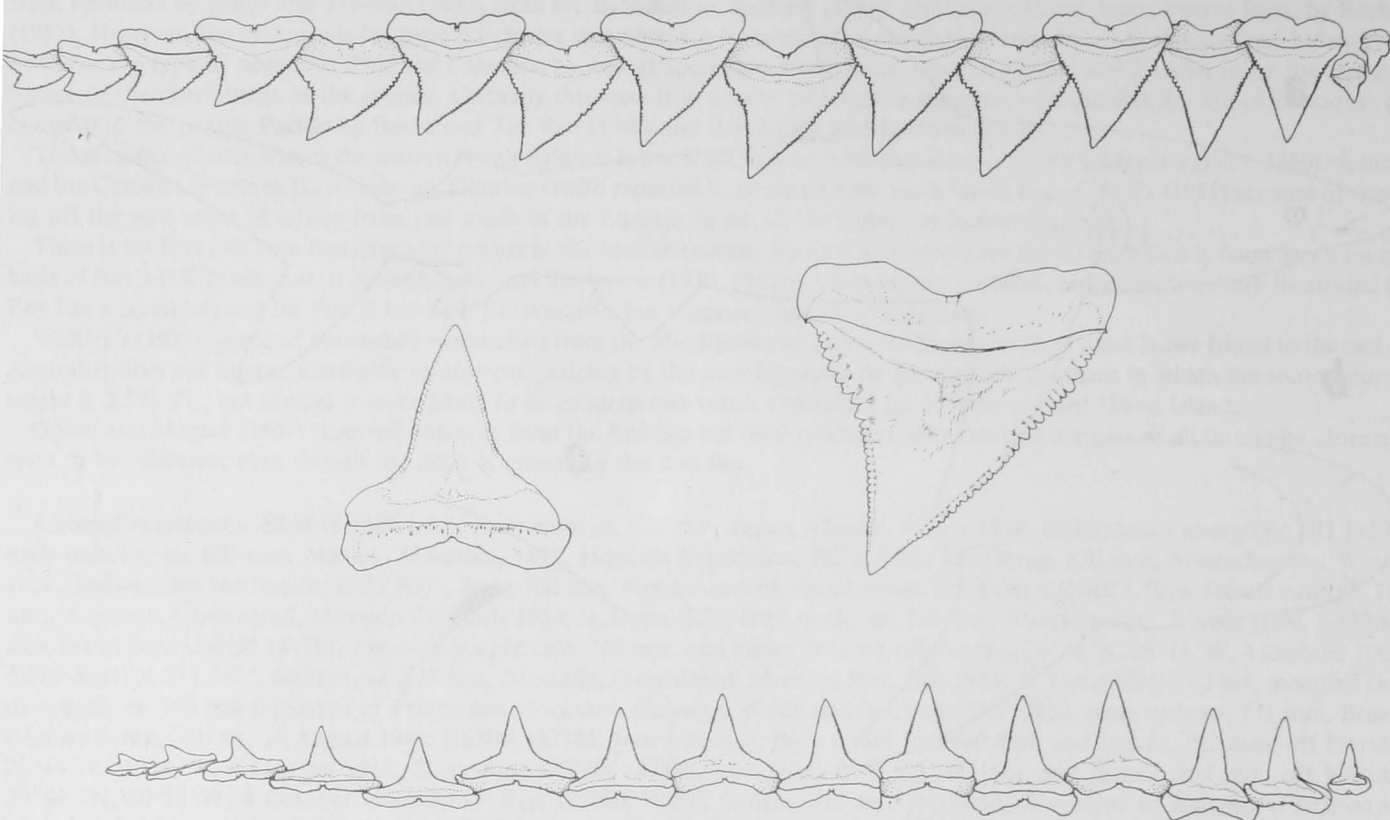


Figure 59.—*Carcharhinus galapagensis*, UCLA 56-236, ca. 2,000 mm TL, from eastern Pacific, Clipperton Island: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

Diagnosis.—Large sharks, up to about 3.00 m long, with a low interdorsal ridge; tips of fins, particularly the pectorals, frequently dusky; snout moderately long and bluntly rounded; internarial width 1.0-1.3 in preoral length; origin of first dorsal fin over posterior third of inner pectoral margin; apex of first dorsal acute to sharply rounded; origin of second dorsal about over anal fin origin; height of second dorsal 2.1-3.3% TL and 1.3-1.7 in length of its rear tip; dental formula usually $\frac{14-1-14}{14-1-14}$ but may be $\frac{13 \text{ to } 15-1 \text{ to } 3-13 \text{ to } 15}{13 \text{ to } 15-1 \text{ to } 3-13 \text{ to } 15}$; upper teeth broad, oblique, concave laterally, with slightly coarser serrations basally; lower teeth erect, serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 103-109; caudal centra 94-107; total centra 200-215; diplospondyly begins from one-third to halfway along pelvic base; diplospondylous centra regular in length; penultimate monospondylous centrum 1.2-1.6 times wider than long.

This species and *obscurus*, *plumbeus*, and *altimus*, differ from all others in having in common an interdorsal ridge, no conspicuous color pattern other than dusky fin tips, and broad upper teeth which are concave but not notched laterally. Both *galapagensis* and *obscurus* have their first dorsal fin origin over or nearer to the pectoral inner corner rather than over or nearer to the pectoral axil as in *plumbeus* and *altimus*. The upper teeth and nasal lobe are also relatively much shorter in *galapagensis* than in *altimus*. The species most likely to be confused with *galapagensis* is *obscurus*. Although these two can clearly be separated on precaudal vertebral numbers (103-109 in *galapagensis*, 86-97 in *obscurus*), they are not so easily distinguished on external features. The first and second dorsal fins of *galapagensis* are, on average, higher than in *obscurus*, and there are differences of comparable value in the relationship between the heights of these fins and the lengths of their rear tips (see under *obscurus*, p. 122). With few exceptions *galapagensis* has been taken only off oceanic islands, and *obscurus* off continental coastlines.

Nomenclatural discussion.—The holotype of *galapagensis* (SU 12324) cannot be found, nor can two of the paratypes, but I have been able to examine the third paratype, an embryo of about 590 mm (SU 12325), which conforms to *galapagensis* as currently recognized. There appear to be no synonyms of *galapagensis*, but there have been problems in distinguishing this species from other eastern Pacific sharks, especially *lamiella* of authors (= *obscurus*), as exemplified by the discussion in Beebe and Tee-Van (1941) and in Rosenblatt and Baldwin (1958). Confusion was also engendered, as pointed out by the latter authors and confirmed here, by the presence of one, and probably two, specimens of *galapagensis* in the type series of *Eulamia platyrhynchus* (= *albimarginatus*) from the eastern Pacific. I have detailed elsewhere in this account (p. 108) that the two paratypes of *Carcharias nesiotes* (= *amblyrhynchus*) from the Hawaiian Islands are also referable to *galapagensis*.

Description (see also Table 63).—Large sharks, growing to at least 3.0 m TL. Midline of back between dorsal fins with a low dermal ridge. Upper precaudal pit strongly developed, lower pit weak.

Table 63.—*Carcharhinus galapagensis*, proportional dimensions in percentage of total length.

	<div> <div>♂ 795 mm</div> <div>♀ 1,572 mm</div> </div>									
	♀ 663 mm	♀ 753 mm	♂ 795 mm	♂ 807 mm	♂ 891 mm	♂ 982 mm	♀ 1,120 mm	♂ 1,572 mm	♂ 2,360 mm	♂ 2,475 mm
	Ecuador	Mexico	Pacific	Mexico	Bermuda		Ecuador	Mexico	Guatemala	Guatemala
	Galapagos Is.	Clarion Is.	Lord	Clarion Is.	CNHM	Hawaiian Is.	Galapagos Is.	Revillagigedo Is.	Champerico	Champerico
	SU 10842	SU 11556	Howe Is.	UCLA 54-242	48374	SU 12790	MCZ 375	USNM 197390	USNM 196824	USNM 196829
Snout tip to										
outer nostrils	3.7	3.9	3.6	3.7	3.6	3.4	3.3	2.7	2.6	2.5
eye	7.1	8.0	7.4	7.7	7.8	7.6	7.1	6.3	6.2	5.7
mouth	7.4	8.1	7.8	8.2	8.1	7.8	7.5	6.8	6.3	6.0
1st gill opening	20.2	21.1	19.1	19.9	20.3	21.8	18.9	18.2	19.3	18.2
3d gill opening	22.5	22.9	20.8	—	22.3	23.9	21.5	20.5	22.6	21.4
5th gill opening	24.4	24.9	22.3	23.8	24.5	25.6	24.1	22.0	24.7	23.2
pectoral origin	23.6	24.5	21.6	22.4	23.4	24.5	22.6	21.4	24.0	22.4
pelvic origin	49.8	48.4	48.8	50.2	50.3	50.2	50.4	49.3	49.3	48.6
1st dorsal origin	30.6	31.2	31.6	31.5	31.5	32.3	31.2	30.2	31.1	29.7
2d dorsal origin	62.9	61.3	61.6	63.6	61.9	63.8	63.6	62.6	63.7	63.4
anal fin origin	63.0	60.4	62.3	63.4	62.3	63.3	62.7	62.9	63.6	63.1
upper caudal origin	73.9	72.3	71.8	72.8	72.5	74.0	73.5	72.8	74.9	74.5
lower caudal origin	73.0	71.3	71.5	72.3	72.0	73.3	72.6	72.3	74.2	73.5
Nostrils										
distance between inner corners	6.2	6.7	6.3	6.6	6.5	6.5	6.2	6.0	6.3	6.0
Mouth										
width	8.4	8.2	8.3	8.9	8.8	9.0	8.5	9.2	8.7	7.8
length	4.6	5.3	4.0	4.5	5.0	5.2	5.0	4.4	5.3	4.5
Labial furrow lengths										
upper	0.6	0.5	0.6	0.6	0.4	0.5	0.4	0.4	0.6	0.4
lower	0.7	0.7	0.5	0.6	0.4	0.7	0.6	0.6	0.7	0.6
Gill opening lengths										
1st	2.6	2.5	2.8	3.0	2.9	2.5	2.6	3.2	2.8	2.6
3d	2.8	3.0	3.1	3.2	3.5	2.9	3.2	3.4	3.2	3.4
5th	2.0	2.5	2.5	2.2	2.8	2.2	2.5	2.6	2.0	2.2
Eye										
horizontal diameter	2.4	2.4	2.3	2.1	2.2	2.1	1.9	1.6	1.3	1.3
1st dorsal fin										
length of base	9.5	8.9	9.0	9.8	10.0	9.3	8.9	9.9	9.9	9.4
length posterior margin	3.5	3.6	4.0	3.8	3.5	3.6	4.3	4.0	4.0	3.7
height	9.5	10.3	10.0	11.2	10.5	10.7	11.1	10.7	11.0	9.6
2d dorsal fin										
length of base	3.5	3.8	3.7	3.1	3.5	3.6	3.0	3.7	4.1	3.5
length posterior margin	3.9	3.9	3.8	4.3	4.0	3.8	3.7	—	3.9	3.9
height	2.6	2.7	2.7	2.7	2.5	2.8	2.8	2.6	2.6	2.6
Anal fin										
length of base	3.8	4.5	4.0	4.3	4.1	4.1	3.9	3.7	4.8	4.2
length posterior margin	3.6	3.7	3.5	3.7	3.6	3.6	3.2	3.9	3.8	3.5
height	2.9	3.1	3.3	3.8	2.9	3.4	3.0	3.3	3.8	3.4
Pectoral fin										
length of base	5.9	5.3	6.0	6.3	5.6	5.9	6.2	6.4	6.6	6.3
length anterior margin	17.8	18.8	17.6	19.7	19.4	20.4	19.6	21.1	22.9	22.6
length distal margin	12.5	15.8	14.8	16.0	16.5	17.0	15.9	17.5	19.1	19.0
greatest width	8.6	9.3	—	9.9	9.2	9.8	9.8	10.4	11.0	10.5
Pelvic fin										
length of base	5.0	5.3	4.9	5.1	4.4	4.9	5.0	5.0	6.8	6.1
length anterior margin	5.7	6.1	5.2	5.9	5.8	5.9	6.2	6.4	6.4	6.0
length distal margin	4.7	5.3	5.3	5.9	5.2	6.0	5.4	6.0	6.1	5.9
length of claspers	—	—	1.8	2.1	2.7	—	—	—	9.2	9.3
Caudal fin										
length of upper lobe	26.1	28.0	28.3	27.7	28.0	27.1	26.3	27.3	27.5	27.2
length of lower lobe	12.5	12.6	13.7	13.5	12.9	12.8	12.8	14.2	14.8	14.5
Trunk at pectoral origin										
width	11.6	11.4	11.1	12.6	11.8	12.1	12.0	13.2	12.3	11.3
height	10.2	10.2	10.1	10.5	—	11.7	10.7	12.7	12.4	11.5
Dental formula		15-1-14	14-1-14	15-1-15	14-1-14	14-1-14		14-1-14		
Vertebrae		15-1-15	14-1-14	15-1-15	14-1-14	14-1-14		14-1-14		
precaudal	106	106	108		104	109		106		
caudal	94	103	102		101	106		100		
total	200	209	210		205	215		206		

¹Syntype of *Eulamia (Platypodon) platyrhynchus* prior to Rosenblatt and Baldwin's (1958) designation of USNM 46847 as lectotype of *platyrhynchus*.

²"Cotype" of *Carcharias nesiotus*.

Dermal denticles close-packed, overlapping, subcircular in small specimens, more nearly rhomboid in larger where they are more or less regularly arranged in diagonal rows; each denticle with three longitudinal ridges and three rather strong posterior marginal teeth in small specimens, but with five to seven ridges in larger specimens and up to five posterior teeth.

Snout moderately long, bluntly rounded in contour, or at most slightly pointed at the extreme tip in small specimens. Anterior margin of eye is slightly forward of front of mouth. Nostrils strongly oblique, slitlike, the anterior margin of each with a low, pointed lobe.

Dental formula $\frac{14-1-14}{14-1-14}$ in 8 of 19 specimens counted; $\frac{14-1 \text{ to } 3-14}{13 \text{ or } 14-1 \text{ to } 3-13 \text{ or } 14}$ in 7; $\frac{14 \text{ or } 15-1-14 \text{ or } 15}{14 \text{ or } 15-1-14 \text{ or } 15}$ in 3; and $\frac{13-1-13}{13-1-13}$ in 1

specimen (SI0 52-107) from the Galapagos. Upper teeth broadly triangular, oblique except for the first one or two series at each side of symphysis, their lateral margins concave in subadults and adults but sometimes weakly notched in juveniles (although the last three or four series at the corner of the mouth have notched lateral margins in adults also), their medial margins varying from straight or nearly so at the center of the mouth to strongly convex towards the corners, both margins rather coarsely serrated, the serrations a little coarser basally, particularly on the lateral margins; one or two (exceptionally three) small symphysial teeth. Lower teeth narrowly triangular, erect except for the last three or four series at the corner of the mouth, both margins finely serrated; one or two (exceptionally three) small symphysial teeth.

First dorsal fin rather high, its apex acute to sharply rounded, its anterior margin only weakly convex in small specimens but moderately convex in large; origin of first dorsal over posterior third of inner (posterior) margin of pectoral fin. Second dorsal fin moderately high and long, almost equal to anal fin, its distal margin concave; length of second dorsal rear tip 1.3-1.7 (mean 1.5) times second dorsal height; origin of second dorsal about over anal fin origin. Pectoral fins moderately long, slender, pointed; origin of pectorals below the level of the fourth gill openings or below and between the levels of the third and fourth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches behind level of first dorsal axil, usually one-third or halfway along the first dorsal rear tip in small specimens but behind the rear tip by a distance of up to the length of the tip in large specimens.

Color in life was described by Kato (1964) as "Dorsal surface and sides plain brownish-gray, sometimes with greenish tinge; sides light gray with metallic green tinge; ventral surface yellowish white; undersides of pectoral fin tips dusky to dark." After preservation in alcohol the back and sides are dark or brownish gray merging to pale or white below; the underside sometimes irregularly mottled; tips and trailing edges of the fins dusky but not black, particularly the undersides of the pectoral fins; small specimens tend to have an overall dusky cast.

Vertebral counts of 6 specimens are given in Table 63 and of another 15 specimens in Table 64. Precaudal counts of 105-109 and total counts of 204-210 for 14 specimens from Walters Shoal, south of Madagascar, are given in Bass et al. (1973).

Centrum diameter considerably greater than centrum length even in longest monospondylous centra at posterior of abdomen. Diplospondylous centrum length regular. Diplospondyly begins above anterior one-third to middle of pelvic base. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.64-0.85 (mean 0.75) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.14-1.44 (mean 1.30) in 15 specimens.

Table 64.—Vertebral numbers in 15 specimens of *Carcharhinus galapagensis*.

Specimens		Precaudal	Caudal	Total
SU 13491	Galapagos Is.	105	99	204
SU 13503	Galapagos Is.	107	95	202
USNM 51213	Galapagos Is.	105	97 +	202 +
USNM 50069	off Costa Rica,			
	Cocos Is.	108	105	213
UCLA 56-236	Clipperton Is.	105	100	205
CNHM 4937	Bermuda	105	107	212
UPR 1140	Virgin Is. ¹	104	90 +	194 +
BMNH 62.6.14	Madeira	104	103	207
BMNH 95.5.28.143	East Atlantic, Gt.			
	Salvage Is.	103	101	204
BMNH 1868.6.15.1	St. Helena	103	104	207
AMS (5 specimens)	Lord Howe Is. ²	106-108	95-100	—
Range (including counts from Table 63)		103-109	94-107	200-215

¹Count supplied by J. E. Randall, Acting Director, Institute of Marine Biology, University of Puerto Rico, Mayaguez, Puerto Rico, pers. commun. April 1963.

²Counts supplied by J. R. Paxton, Curator of Fishes, The Australian Museum, 6-8 College Street, Sydney, New South Wales, from specimens collected in February 1973. Pers. commun. September 1973.

The smallest, apparently free-living specimen I have seen was 665 mm TL, while the largest embryo was 590 mm. The type of *galapagensis* was stated to be an embryo, 650 mm long (Snodgrass and Heller 1905). Of the few males studied here, five up to 1,016 mm were clearly immature, with clasper lengths ranging from 1.8 to 2.7% TL, and two others of 2,360 and 2,475 mm were mature with clasper lengths of 9.2 and 9.3%. The largest specimen seen was a female of 2,550 mm from the Hawaiian Islands, which was only slightly shorter than a pregnant female of 2,592 mm recorded by Fowler (1932) from the eastern Pacific (Cocos Island). This size, i.e., about 2.6 m, is generally in accord with the statement by Snodgrass and Heller (1905) when first describing the species that "The adults average 6 to 8 feet in length." However, Kato et al. (1967) reported that *galapagensis* grows to about 3.7 m, but this estimate is seeming-

ly not based on actual measurements and may be derived from Limbaugh's (1963) observations at Clipperton Island where "Specimens 10 to 12 feet long . . . were thought to be adults of this species." Kato and Carvalho (1967) stated that *galapagensis* "may attain a length of about 250 cm" (body length) which would represent a total length of about 3,250 mm. If the identification of a Virgin Island specimen is correct (see Randall 1963a and remarks under *Distribution* in the present account, p. 131), then the 2,920 mm male recorded there is larger than any other specimen for which definite measurements are available. Published data on reproductive biology of *galapagensis* are few. Limbaugh (1963) suggested that young at Clipperton Island are born at lengths of "2 to 2½ feet" (about 600 to 750 mm). The smallest free-living specimen tagged by Kato and Carvalho (1967) in the eastern Pacific had a body length of 44 cm, which would mean a total length of about 595 mm. Tester (see footnote 4) reported that 10 pregnant females from the Hawaiian Islands had litters ranging from 6 to 16, with a mean of 9.5. Size at maturity in the female is probably reached at not less than about 2,500 mm TL, judging by Fowler's (1932) record above of a pregnant female of 2,592 mm and Limbaugh's (1963) data on 32 immature females up to 2,350 mm. Males, like those of other *Carcharhinus* species, undoubtedly mature at a smaller size; Limbaugh (1963) recorded them as immature up to 2,050 mm, while the smallest mature male seen in the present study was 2,360 mm.

Distribution (see also Material examined).—For more than half a century following its original description, *galapagensis* was not known to occur outside the eastern Pacific. However, records now show that it has a scattered but widespread, virtually circumglobal distribution in the tropical warm temperate zone, with the added unusual feature that it is, in general, associated with oceanic islands. The abundance of the species around oceanic islands was first commented on by Snodgrass and Heller (1905), the authors of *galapagensis*, who noted that it was "Extremely abundant about the Galapagos Islands We examined a large number of them, several hundred being taken aboard the schooner, and we saw probably thousands in the water." Similar remarks were made by Herre (1936)—"This shark swarms in the waters of the Galapagos Islands and about Cocos Island. I have never seen sharks of this genus in such abundance as in these two localities"—while later, Beebe and Tee-Van (1941) were to note that "all locality records of . . . *galapagensis*, with the exception of a single questionable continental record . . . are off-shore and insular."

My data, supplemented by literature records from Limbaugh (1963) and Kato et al. (1967) for the eastern Pacific, Tester (1969 see footnote 4) and Randall (1973, 1974) for the central Pacific, Bryan (1973) for Guam Island, D'Aubrey (1964) and Bass et al. (1973) for the western Indian Ocean, and Randall (1963a) for the Caribbean, give *galapagensis* a distribution as follows: eastern Pacific islands from the Revillagigedo Islands southwards to the Galapagos Islands, including Clipperton, Cocos, and Malpelo Islands, and open-ocean localities off southern Baja California, Guatemala, and Colombia; central Pacific at the Hawaiian Islands (including also Laysan Island and Pearl and Hermes Reef to the northwest) and at Pitcairn Island, Ducie Island, and Rapa to the south (Randall 1973, 1974); western Pacific in the north at the Marianas (Guam) and in the south at the Kermadec Islands, Lord Howe Island, and probably also at the Middleton and Elizabeth Reefs, north of Lord Howe, judging by measurements of a specimen reported by Whitley (1944, as *macrurus*); southwestern Indian Ocean at Walters Shoal (lat. 33°07'S), south of Madagascar; eastern Atlantic islands from Madeira in the north to St. Helena in the south, and including Gt. Salvage Island and Ascension; and the western North Atlantic at Bermuda, and probably in the Caribbean at the Virgin Islands where Randall (1963a) has reported on an adult male specimen²¹ responsible for a fatal attack on a swimmer. Finally, it is worth noting that Rey's (1928) account of a ridge-backed shark, under the name *commersoni*, as part of the Iberian fauna could well be interpreted as being of *galapagensis*. The locality for the specimen illustrated was not given, but Rey mentioned supplementary material (skin and jaws) from Alicante on the Mediterranean coast of Spain.

The extent to which *galapagensis* occurs in the open ocean rather than in association with oceanic islands needs further investigation. Kato et al. (1967) noted that "... large individuals [are] also found on the high seas (off Colombia and Guatemala, and on banks off southern Baja California), and sometimes close to the continental shore . . ." and this is in accord with two specimens, adult males, from off Guatemala, provided for my study by S. Kato.

However, Strasburg (1958), in reporting on the distribution and abundance of 6,118 specimens of pelagic sharks taken in a longlining program in the central Pacific, more or less centered on the Hawaiian Islands and extending to lat. 50°N and 20°S, did not encounter *galapagensis*, though it is now evident from Tester's (see footnote 4) inshore longlining program at the Hawaiian Islands that *galapagensis* is one of the more common large sharks close to the islands.

Material examined.—BMNH 1901.6.28.251-252, two males, 580 mm (embryo) and 745 mm, Galapagos Islands, from Stanford University; SU 12325, embryo, ca. 590 mm (paratype of *Carcharias galapagensis*), Galapagos Islands, 1898-99, E. Heller and R. E. Snodgrass; SMF 5221, embryo or newborn male, ca. 650 mm, Galapagos Islands, Indefatigable Island, 1957, I. Eibl-Eibesfeldt; SU10842, embryo or newborn female, 663 mm, Galapagos Islands, Chatham Island, *Albatross*; USNM 41278, male, 665 mm, Galapagos Islands, Chatham Island, 1888, *Albatross*; AMNH 15689, male, 728 mm, Mexico, Revillagigedo Islands, Clarion Island; SIO 52-107, female, 735 mm, Galapagos Islands, Santa Cruz Island, Academy Bay, 10 August 1952, R. Wisner; SU 11556, female, 753 mm (originally a syntype of *Eulamia platyrhynchus*), Mexico, Revillagigedo Islands, Clarion Island, 1888-89, *Albatross*; DM 5942, male, 760 mm, Lord Howe Island, February 1973, Australian Museum; UCLA 56-236, two males, 768 and 795 mm, and two females, 778 and 912 mm, Clipperton Island, 22-29 October 1956, W. J. Baldwin et al.; BMNH 1868.6.15.1, male, 772 mm, St. Helena, J. C. Mellis; USNM 50069, male, 775 mm, Costa Rica, Cocos Island, July 1889, R. E. Snodgrass and E. Heller; SU 13491, male, 783 mm, Galapagos Islands, Albemarle Island, Tagus Cove, 9 January 1929, A. W. Herre; UCLA 55-155, female, 787 mm, Mexico, Revillagigedo Islands, Socorro Island, 3 May 1955; NZOI 80, male, 792 mm, Kermadec Islands, Macauley Island, NZOI Stn. K835, 28 July 1974; AMS I.5426, male, 795 mm, Lord Howe Island, 2 February 1903, Waite and McCulloch; USNM 51213, female, 800 mm, Hawaiian Islands, 1901; UCLA 54-242, male, 807 mm, Mexico, Revillagigedo Islands, Clarion Island, 27 March 1954; SU 13503, male, 808 mm,

²¹Data from this specimen (measurements, vertebral count, and photographs) and fragments including the jaws and other items listed here under Material examined conform closely to *galapagensis* although the teeth differ slightly in shape from eastern Pacific material (see Fig. 59) and the pectoral fin is relatively too short; further specimens, particularly of adults, are needed to confirm this identification.

Galapagos Islands, Albemarle Island, Tagus Cove, 9 January 1929, A. W. Herre; AMS IA.732, female, 810 mm, Lord Howe Island, 10 July 1922, R. Baxter; CNHM 4937, male, 815 mm, Bermuda; BMNH (uncat.), male, 817 mm, Ascension Island; BMNH 95.5.28.143, male, 827 mm, eastern Atlantic, Gt. Salvage Island, Baring and Grant; BMNH 79.5.14.404, male, 838 mm, Ascension Island, *Challenger*; BMNH 72.8.28.60, male, 858 mm, Bermuda, J. M. Jones; USNM 196795, male, 870 mm, Mexico, Revillagigedo Islands; Socorro Island, 20 January 1962, U.S. Fish and Wildlife Service; BMNH 62.6.14, female, 890 mm, Madeira; CNHM 48374, male, 891 mm, Bermuda; USNM 41276, male, 892 mm, Galapagos Islands, 1888, *Albatross*; ORID 562, female, 965 mm, South Madagascar Ridge, Walters Shoal, 33°09'S, 43°51'E, February 1963; SU 12790, female, 982 mm ("cotype" of *Carcharias nesiotes*), Hawaiian Islands, Laysan Island, 1902, *Albatross*; UMMZ 172421, female, ca. 1,000 mm, Bermuda, St. Georges Island, 2 mi SSW of North Rock, 19 June 1951, R. Bailey et al.; MCZ 375, male, 1,016 mm, and female, 1,120 mm, Galapagos Islands, Charles Island, 1872, Hassler Expedition; NZOI 81, female, 1,135 mm, Kermadec Islands, Curtis Island, NZOI Stn. K865, 31 July 1974; NMV 61.445, male, ca. 1,250 mm, Hawaiian Islands, Pearl and Hermes Reef, February 1928, Pietschmann; USNM 196797, female, 1,500 mm, Mexico, Revillagigedo Islands, Socorro Island, 8 January 1962, F. Hester et al.; USNM 197390, female, 1,572 mm, Mexico, Revillagigedo Islands, Socorro Island, 5 August 1962, S. Kato; USNM 196824, mature male, 2,360 mm, Guatemala, Champerico, 14°22'N, 92°48'W, 3 February 1962, S. Kato et al.; USNM 196829, mature male, 2,475 mm, Guatemala, Champerico, 14°28'N, 92°58'W, S. Kato et al.; USNM 196600, jaws, skin sample, and measurements of female, 2,550 mm, Hawaiian Islands, Oahu, off Kewalo Basin, July 1961, Hawaii State Fish and Game; UCLA 56-236, jaws of specimen ca. 2,000 mm, Clipperton Island, 22-29 October 1956, W. Baldwin et al.; UPR 1140, jaws, measurements, photographs, and fragments of mature male, 2,920 mm, Virgin Islands, St. Thomas, Magens Bay, 21 April 1963, U.S. Navy; also SU 32027, jaws only, (paratype of *Carcharias nesiotes*) Hawaiian Islands, Mokapu Islet, 30 April 1902, *Albatross*.

Carcharhinus plumbeus (Nardo, 1827)

Figures 60, 61, 62

Squalus plumbeus Nardo, 1827:477, 483. No specimens mentioned.

Carcharias (Prionodon) milberti Valenciennes in Müller and Henle, 1841:38-39, 189, pl. 19 (teeth). Three specimens listed after the description, as follows: 1 spirit specimen, Berlin Museum, from Hemprich and Ehrenberg; 1 in the Leiden Museum; 1 spirit specimen, Paris Museum, from New York through Milbert. One further specimen (adult) in the Vienna Museum is listed in a supplement on p. 189. Mediterranean and Oceanic.

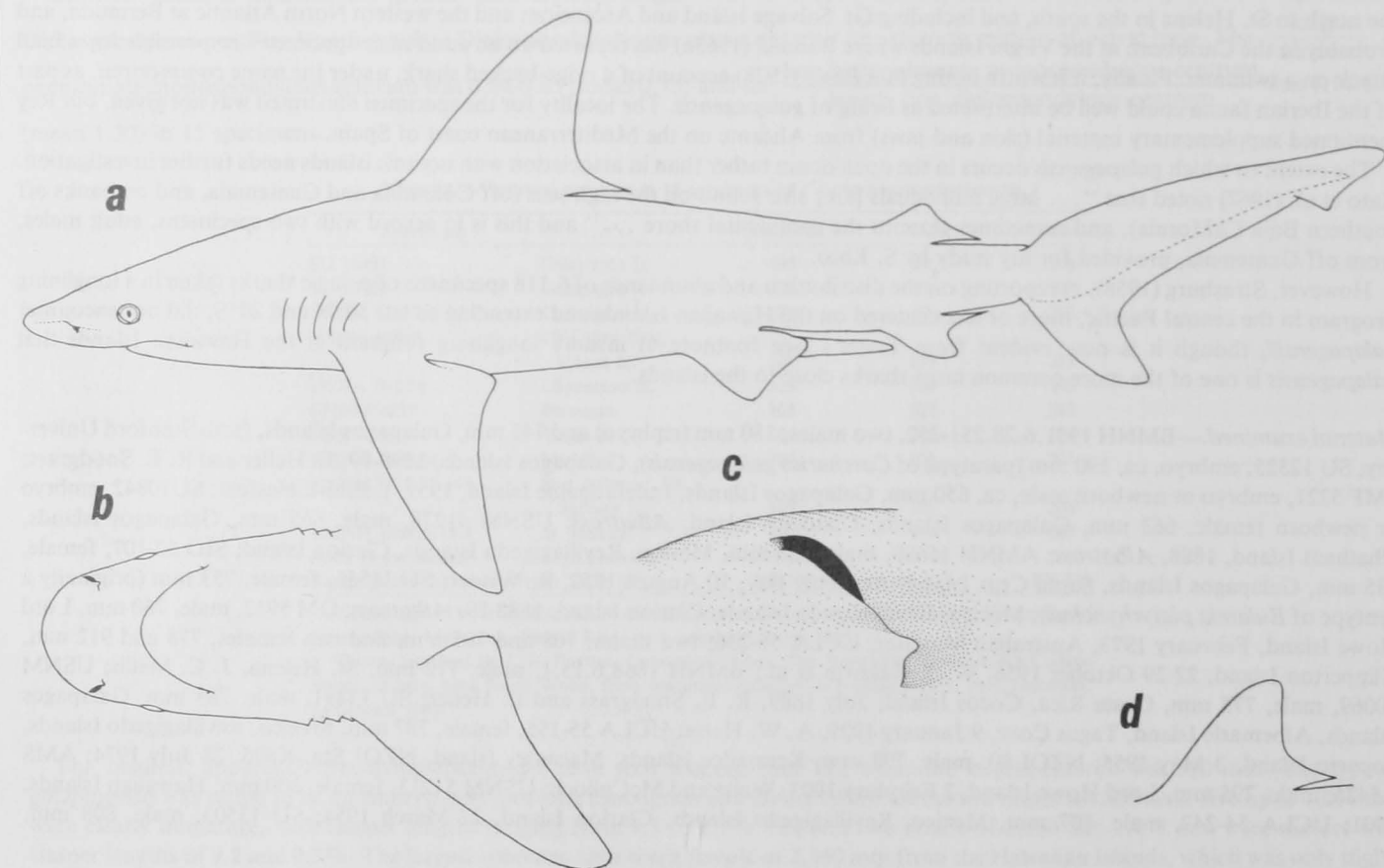


Figure 60.—*Carcharhinus plumbeus*, USNM 196594, 1,445 mm TL, male from Hawaiian Islands: a, left side; b, underside of head; c, enlarged left nostril; d, first dorsal fin of USNM 89256, 650 mm TL, female from western North Atlantic.

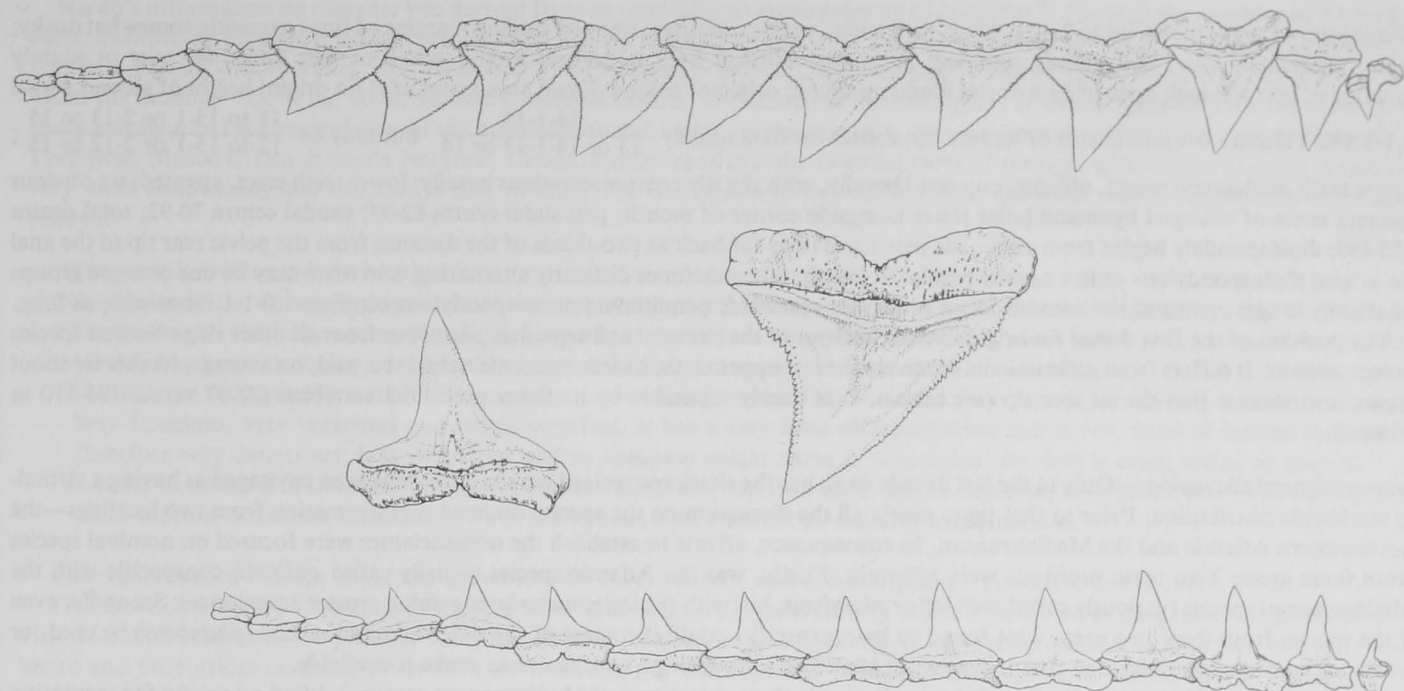


Figure 61.—*Carcharhinus plumbeus*, USNM 196599, 1,670 mm TL, female from Hawaiian Islands: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

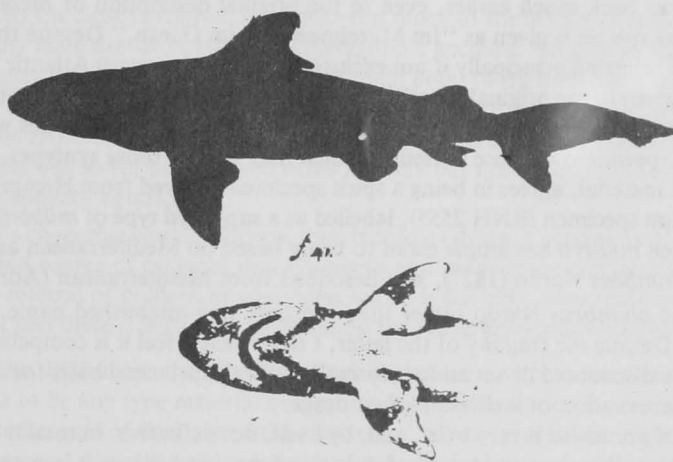


Figure 62.—Reproduction of two figures from an unpublished manuscript by Chiareghini in the Marciana Library of Venice. The figures are referred to in that part of the manuscript headed "Sp. 7. fig. 40.41 *Squalus Chaecchia nostro*."

- Carcharias ceruleus* De Kay, 1842:349-350, pl. 61, fig. 200. Description and illustration of specimen 25 in (635 mm) long, presumably from New York although De Kay states that it extends to New Hampshire.
- Lamna caudata* De Kay, 1842:354, pl. 62, figs. 205, 205a, 205b. Description and illustrations of specimen 7 ft 4 in (2,235 mm) long from the Rhode Island coast; specimen captured and illustrated by Carson Brevoort.
- Carcharias (Prionodon) japonicus* Temminck and Schlegel, 1850:302, pl. 133. The only material mentioned are jaws ("des mâchoires") and a figure, all sent by Burger. The figure was said to be of a fresh specimen 4½ ft (1,372 mm) long. Japan.
- Carcharias obtusirostris* Moreau, 1881:332-335, text figs. 53-54. No specimens listed but size said to be from 2.0 to 4.0 m; a young individual, size not stated, is mentioned several times in the description; Mediterranean, common at Cette, rare at Nice.
- Carcharhinus stevensi* Ogilby, 1911:38-39. Two specimens, erroneously stated to be 164 and 187 mm long rather than 164 and 187 cm; Australia, Queensland, Bustard Bay and NorWest Inlet.
- Carcharinus latistomus* Fang and Wang, 1932:235-236, fig. 9. Holotype, sex not stated, "565 mm to last vertebra," China, Tsingtau.
- Galeolamna dorsalis* Whitley, 1944:256-257, fig. 3. "Photographs of specimens," up to about 5 ft (1,524 mm), were the only material. Western Australia, Carnarvon.

Diagnosis.—Large sharks, up to 2.40 m long, with a low interdorsal ridge; tips and trailing margins of fins frequently somewhat dusky; snout moderately short and bluntly rounded; internarial width 0.9-1.3 in preoral length; origin of first dorsal fin over or slightly anterior to pectoral axil; apex of first dorsal bluntly pointed; origin of second dorsal about over anal fin origin; height of second dorsal 2.1-3.5% TL and 1.0-1.6 in length of its rear tip; dental formula usually $\frac{14-1-14}{13 \text{ or } 14-1-13 \text{ or } 14}$ but may be $\frac{13 \text{ to } 15-1 \text{ or } 2-13 \text{ to } 15}{12 \text{ to } 15-1 \text{ or } 2-12 \text{ to } 15}$;

upper teeth moderately broad, oblique, concave laterally, with slightly coarser serrations basally; lower teeth erect, serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 82-97; caudal centra 70-92; total centra 152-189; diplospondyly begins from above the pelvic axil to as far back as two-thirds of the distance from the pelvic rear tip to the anal fin origin; diplospondylous centra usually regular in length, but sometimes distinctly alternating, and there may be one or more groups of slightly longer centra at the second dorsal or farther rearward; penultimate monospondylous centrum 1.0-1.1 times wide as long.

The position of the first dorsal fin origin over or in front of the pectoral axil separates *plumbeus* from all other ridge-backed species except *altimus*. It differs from *altimus* in its relatively shorter upper teeth, its less attenuate nasal lobe, and, on average, its shorter snout region and shorter first dorsal rear tip (see tables). It is clearly separable by its fewer precaudal vertebrae (82-97 versus 101-110 in *altimus*).

Nomenclatural discussion.—Only in the last decade or so has the shark recognized here as *plumbeus* been envisaged as having a virtually worldwide distribution. Prior to that time, nearly all the discussion on the species centered on information from two localities—the northwestern Atlantic and the Mediterranean. In consequence, efforts to establish the nomenclature were focused on nominal species from these areas. Two main problems were apparent. Firstly, was the Atlantic species (usually called *milberti*) conspecific with the Mediterranean species (variously called *milberti* or *plumbeus*, but with the latter name later gaining greater acceptance). Secondly, even if the species from these two areas were found to be conspecific, could the name of the older nominal species (*plumbeus*) be used, or was it so inadequately described that it cannot be identified with enough confidence to make it available.

In the present study, and admittedly using a small sample (four specimens) of Mediterranean material, I find no reason for separating the Mediterranean and North Atlantic populations. Springer (1950), by implication, suggested that they differed in their dermal denticles, but I cannot confirm this difference as a constant character. Although there are differences in the appearance and spacing of denticles between some samples or specimens from different localities, and of different sizes or ages, they are not consistently distinctive enough to be of obvious diagnostic value.

The view that the Mediterranean and Atlantic populations are conspecific is by no means new. In recent years it has been espoused by Tortonese (1950, 1951b), but it dates back much earlier, even to the original description of *milberti* by Valenciennes in Müller and Henle (1841) where the range for the species is given as “Im Mittelmeer und im Ocean.” Despite this, the name *milberti* has generally been accepted as being based on, or referring principally if not exclusively to, northwestern Atlantic material, probably because the only syntype for which a locality was given in the original description was that from New York, collected by Milbert. This syntype, in the Paris Museum, was selected as lectotype of *milberti* by White et al. (1961). Two other syntypes were stated to be in the Berlin and Leiden Museums; I have examined specimens in those museums which may well be those syntypes. That in the Berlin Museum (ISZZ 4467), although not labelled as type material, agrees in being a spirit specimen received from Hemprich and Ehrenberg. Its locality was “Italy, Trieste.” The Leiden Museum specimen (RNH 2555), labelled as a supposed type of *milberti*, was from Livorno, Italy. If these specimens are, in fact, syntypes, then *milberti* has ample claim to being based on Mediterranean as well as Atlantic material. By contrast, the other nominal species, *plumbeus* Nardo (1827), was described from Mediterranean (Adriatic) material only.

Use of the poorly founded name *plumbeus* Nardo rather than the later well-established name *milberti* Valenciennes can only be upheld by circumstantial evidence. Despite the fragility of the latter, I nevertheless feel it is compelling enough to warrant full recognition. The name *plumbeus* cannot be discounted or set aside informally, and the principal basis for any argument to replace it with the name *milberti* would have to be conservation of well-established usage.

Nardo's original account (1827) of *plumbeus* is very brief, and, by itself, not definitive. In total it 1) lists *plumbeus* (p. 477) as species No. 24, plus the vernacular name *Caecchia*, in a treatment of Adriatic fishes, and places it in a section of the genus *Squalus* lacking spiracles, and 2) describes it (on p. 483) as “Speciei secundae convenit perfecte *Squ. glaucus* Bloch si colorem exciperetur et formam rostri quae in exemplari nostro rotunda est.” No type material of *plumbeus* is known to exist.

Nardo's above comparison of *plumbeus* with *Squalus glaucus* (= *Prionace glauca*, the blue shark), in which he distinguishes the former only by color and snout shape, does not engender confidence in his ability to discriminate species, for these two species are markedly different in many other obvious ways.

Arguments (Tortonese 1950, 1951b) for the view that, despite the poor description, the name *plumbeus* is valid and refers to *milberti* or a Mediterranean form of *milberti* are principally that 1) Nardo himself later (1853) synonymized *milberti* with *plumbeus*, and 2) that “*milberti*” is the only species of *Carcharhinus* in Italian seas. With respect to argument (1), one could query the strength of this evidence in the light of Nardo's earlier seemingly poor ability to discriminate between the blue shark and his *plumbeus*. Argument (2) is not valid, because my data show that a second species, *brachyurus*, is also present (see p. 171 of this account).

If the above were the only evidence, then use of the name *plumbeus* as a senior synonym of *milberti* would be very arbitrary, as strongly indicated by Springer (1960). However two other references to *plumbeus* by Nardo (1847a, b), and the material on which they were based, throw further light on the matter and provide more confidence in the identity of *plumbeus*. The 1847a paper lists *plumbeus* and gives as a synonym of it “*Sq. caecchia*, Ch., fig. 40, 41.” It also tabulates other information including size (“7 piedi ed oltre.”), habitat (“Canali profondi.”), availability in the fishery (“Estate non frequente.”), fishing method (“A *togna* accidentalmente.”), and use (“Benchè non molto pregiato, è buono, e mangiasi arrosto o allessa”). The 1847b paper simply synonymizes *plumbeus* Nardo with “*Squal. Caecchia*, Ch.” These papers are the only published source of the name *Squalus caecchia* which later authors have attributed to Nardo, though it is clear enough that the authorship should be Chierighini in Nardo. The name *caecchia* is, however, not available in that it was first published as a synonym, and has subsequently always been regarded as a synonym of *plumbeus*.

Nardo's information on *caecchia* was derived from an unpublished manuscript by Chiareghini.²² Through the courtesy of Alvise Barbaro, Istituto de Biologia del Mare, Venice, who located the manuscript in the Marciana Library of Venice, I obtained a copy of that part of it dealing with *caecchia* (spelt *chaecchia* by Chiareghini). This includes a lengthy (4 pages) handwritten account of the species, under the heading "Sp. 7. fig. 40.41. *Squalus Chaecchia* nostro," and a copy of the two figures of which figure 40 is a lateral view of the shark and figure 41 is a ventral view of the head back to and including the pectorals. These figures are reproduced here as Figure 62. E. Tortonese, Museo Civico di Storia Naturale, Genoa, kindly translated the essential parts of the text, which apart from its length is in very small handwriting and not always easy to read. The description is very verbose, and the most important points from it are as follows:

"The orbit is well rounded and large."

"On the back, the dorsal fin begins above the end of the pectoral base and in this point falls the maximum height of the body."

"The surface of the body under the paired fins and on the belly is white and the other surface is ash gray with a silvery shade."

"All the skin is rough, being covered with a fine shagreen, and is also all covered with mucus."

"This fish not only inhabits our Gulf (Venice) but is also found on the deep bottoms of our lagoon. According to the fishermen it is very ferocious, very voracious and swims very fast. It has a very keen olfactory sense and is very fond of human flesh, being therefore very dangerous. It is viviparous and its common vulgar name is 'Chaecchia.' Its flesh is eaten boiled or roasted."

"In order to define it in Linnean fashion I shall write *Squalus Chaecchia* caput latiore depresso, extremitate rostri obtusa subrotundata, capsulis oculorum rotundatis; ore in mandibulis tribus ordinibus dentium triangularium."

Chiareghini stated that his *chaecchia* grows to 8-9 "piedi veneti," and according to E. Tortonese this is about 2-3 m.

The above description, coupled with Chiareghini's figures, agree, in general, very well with *milberti*. In particular, the position of the first dorsal fin relative to the pectoral base, the eye size, relative size and positions of the second dorsal and anal fins, and the overall shape and proportions conform better to *milberti* than to any other species. The shape of the snout in ventral view is, perhaps a little too pointed but is, nevertheless, feasible if the illustration was of a newly born or juvenile specimen—and this would seem to be the case judging by the size and shape of the first dorsal and pectoral fins. The hearsay reference to the species being very ferocious and very fond of human flesh, is disquieting with respect to *milberti*. Such behavior could more aptly be ascribed to *leucas*, at least in parts of its geographic range, and *leucas* is one of the relatively few species which has its first dorsal fin placed over the end of the pectoral base as does the shark in Chiareghini's figure. However, *leucas* has too short and blunt a snout, and too small an eye, to fit Chiareghini's figures, and is not definitely known from the Mediterranean.

It is worth noting that, judging by the close correspondence between much of the information presented in Chiareghini's manuscript and in Nardo (1847a), Nardo must have drawn heavily on Chiareghini's account, suggesting that he was well satisfied on the conspecificity of his *plumbeus* and Chiareghini's *chaecchia*. Lastly one could point to the indication from the vernacular names, although I am unable to assess the weight of this indication. Nardo (1827) used *Caecchia* for *plumbeus* in his first description of the species, and repeated this in 1847b and 1853; his 1847a use of *Caecchia* was probably a lapsus calami. If Nardo did not see Chiareghini's manuscript until after 1827—and I presume this was so for he mentions other authors but not Chiareghini—the similarity between Nardo's *Caecchia* and Chiareghini's *Chaecchia* appears significant.

If it is accepted that Chiareghini's *chaecchia* equals *milberti*, then Nardo's (1847a, b) accounts of *plumbeus* incorporating *caecchia* as a synonym thereby provide a second source of evidence that *plumbeus* and *milberti* are conspecific; and this evidence is seemingly independent of Nardo's later (1853) referral of *milberti* to *plumbeus*, which is the only other real basis for validating *plumbeus*. Because of this second source of evidence I feel there is sufficient justification for recognizing *plumbeus* as a valid senior synonym of *milberti*.

De Kay's *ceruleus*, described in his 1842 account of the New York fauna, can, with reasonable confidence, be ascribed to *plumbeus* even though there does not appear to be any type material to confirm it. The description is very general, but mentions the first dorsal origin as being "... over the posterior part of the base of the pectorals ..." and this is borne out in the illustration. The latter agrees well with *plumbeus* except for the second dorsal fin which is too low and which as shown would better characterize *obscurus*. However, identification as *obscurus* can be discounted because of the forward position of the first dorsal fin and the size of the specimen (635 mm TL); De Kay does not state that it was, or could be, an embryo, hence if free living it is an appropriate size for a recently born *plumbeus* but much too small for *obscurus*.

According to De Kay (1842) he described his *caudata* as a species of *Lamna*, rather than *Carcharias*, because all its gill openings were anterior to the base of the pectorals. Evidently De Kay arrived at this generic placement from a study of the illustration of his species made from a large (2,235 mm) specimen by Carson Brevoort who was also responsible for catching the specimen off Rhode Island. If it is accepted that the illustration is in error in this respect, then *caudata* is clearly a species of *Carcharhinus*, and judging by both the description and the illustrations (including a view of the underside of the head and one upper tooth as well as the lateral view of the whole shark) can be identified as *plumbeus*. In particular the description mentions (and the lateral view shows) the first dorsal fin originating "... over about the middle of the base of the pectorals," and this feature in conjunction with the shape of the snout and the upper tooth indicates *plumbeus*.

The description itself contains several obvious errors; the second dorsal fin is stated to be "... 0.3 high, with a base half an inch long ..." and interpreting the 0.3 as inches (as in other descriptions in the same account) would give the "... seven feet four inches" long

²²Abate Stefano Chiareghini (1745-1820). I do not have the title of the manuscript and the only part of it that I have seen is the excerpt mentioned above. It may be the same as that published posthumously, i.e., Chiareghini, S. 1870. *Ipsa Chiareghini conchyliia ovvero contribuzione pella malacologia Adriatica desunta dal manoscritto descrizione de' crostacei, de' testacei, et de' pesci abitano le lagune e golfo Veneto, rappresentati in figure, a chiaroscuro ed a colori dall' Abate S. Chiareghini ... illustrata da S. Brusina, Pisa*, but I have not seen this either.

able to be made before other evidence became available to confirm that *brachyurus* is present in the Mediterranean. Subsequent analysis of data on proportional dimensions shows that the measurements given by Moreau (1891) for his embryos point clearly to both of them being *brachyurus*. In particular, the length of the first dorsal base separates *brachyurus* from *plumbeus* as indicated in Table 65 where Moreau's measurements are also given for comparison.

Table 65.—Length of first dorsal fin base as percentage of total length in *Carcharhinus brachyurus* and *C. plumbeus*, and comparable data from Moreau's (1891) account of *C. obtusirostris* and *C. milberti*.

	Data from present study		Data from Moreau (1891)		
	<i>brachyurus</i> 16 specimens 650-2,725 mm TL	<i>plumbeus</i> 15 specimens 390-1,670 mm TL	" <i>obtusirostris</i> " 1 embryo 420 mm TL	" <i>milberti</i> " 1 embryo 410 mm TL	" <i>milberti</i> " New York syntype 610 mm TL
First dorsal base as % TL					
Range (mean)	8.9-10.8 (9.7)	11.1-13.8 (11.9)	9.5	8.8	11.1

A further complication is presented by Moreau's (1891) description of *milberti*. The description is based partly on the New York syntype of *milberti* and partly on other specimens which, except for the embryo discussed above, are not itemized other than in terms of their general size, e.g., "très-grande taille, moyenne taille, adultes, jeunes," etc. Judging by Moreau's illustrations of the teeth (his figures 221 and 222, and especially the latter) and the dental formula he gave $\frac{15-1-15}{15-1-15}$, there is no doubt that some of these other specimens and perhaps all of them were *brachyurus* rather than *milberti*. This misidentification which Moreau made provides the clue needed for understanding why he should have described *obtusirostris* as a species separate from *milberti* (*plumbeus*). He did so because, in general, his *milberti* equals *brachyurus* and his *obtusirostris* equals *plumbeus*. This interpretation is satisfactory but it raises one nomenclatural difficulty. Compagno (1973b) listed as holotype of *obtusirostris* the 420 mm male embryo (MNHN 98-1227) for which Moreau (1891) gave measurements, thus more firmly categorizing its status than did Tortonese (1951b) who presumed it was the type. However, if this designation were accepted it would make *obtusirostris* a junior synonym of *brachyurus*, which is at variance with Moreau's (1881) account in which he was clearly, if not exclusively, dealing with *plumbeus*. The situation can best be met by disregarding Compagno's listing on the grounds that there is no definite evidence to establish that MNHN 98-1227 is either a holotype or type material at all. Moreau (1881) did not list the specimen, although it may have been the "jeune individu" he mentioned in the description. Ch. Roux informs me that MNHN 98-1227 was catalogued in 1898 along with the rest of Moreau's collections which were given to the museum following his death in 1896. Catalogue data do not show when the specimen was collected. It is conceivable that it was not collected until after 1881 along with the other similar-sized embryos (MNHN 98-1228, 98-1229) which Moreau treated as *milberti* and one of which he listed along with MNHN 98-1227 in 1891. It is clear from Moreau's (1881) text on *milberti* that he did not have these "*milberti*" embryos at that time.

Ogilby's (1911:38) description of *stevensi*, based on two specimens from Queensland, Australia, was not illustrated, and the type material originally held in the Queensland Museum appears to have been lost according to McCulloch in Whitley (1934) who also noted that the lengths of the two specimens (164 and 187 cm) were erroneously given in millimeters rather than centimeters. A further oversight by Ogilby was in heading his description on page 38 as "*Carcharias stevensi*" rather than as "*Carcharhinus stevensi*." That he intended the latter is evident in his introduction on page 36. The description, which is reasonably good and includes many proportional measurements, has been variously interpreted by later authors. For example, Whitley's (1940) account of *stevensi* is referable to *leucas* whereas his 1943 interpretation appears to be *obscurus* and his 1964 descriptions apply to *plumbeus* (Gillett Cay specimen) and some other species (Capre Cay specimen).

Ogilby (1911) regarded *stevensi* as distinctive in the "... extreme shortness of the postventral portion of the body ..." but I do not find this to be a very useful diagnostic character. A more important item in the description is the vertical height of the first dorsal fin. Ogilby gave this as 1.25-1.33 in the length of head, and the latter as 4.9 in the total length; if these proportions are converted, then the first dorsal height ranged from 15.3 to 16.3% TL. From figure 5 it can be seen that the only two species which have or approach these high values are *plumbeus* and *longimanus*. The latter can be discounted in terms of its color pattern, the shape of the first dorsal fin apex, and in some proportional dimensions. On the other hand, agreement between *plumbeus* and *stevensi* is, in general, very good, and this, coupled with the fact that *plumbeus* occurs in Queensland waters, is sufficient to leave little doubt that they are conspecific. The chief disquieting feature at first glance is Ogilby's statement that in *stevensi* the eye is "... inserted midway between the tip of the snout and the second gill-opening. ..." However, apart from this not occurring in any species of *Carcharhinus* the statement does not agree with another item in the description that the snout length (i.e., preocular) is "... 1.7 in the space between the eye and the first gill-opening. ..." This latter item is perfectly feasible for *plumbeus* but obviously would not permit the eye to be anywhere near to midway between snout tip and second gill opening. Other minor differences between *stevensi* and *plumbeus* are in the description of the lower teeth. Firstly, the number of 15-0-15 is improbable for *plumbeus* but could be explained by Ogilby counting symphysial teeth as laterals—on this basis a formula of 14-2-14 is possible. Secondly, the lower teeth were described as "entire" (i.e., smooth edged) but this may only mean that their fine serrations were overlooked.

Fang and Wang's (1932) account of *latistomus* as a new species from China agrees well enough with *plumbeus* for me to refer it to that species, although the description is rather general and no dental formula or illustration of the teeth is given. The account, including two illustrations, was based only on the holotype, a juvenile of "... 565 mm. to last vertebra," deposited as No. 11156 in the Museum of the Biological Laboratory of the Science Society of China; I do not know if this holotype is still in existence. The only diagnostic

comparison made by Fang and Wang was to state that their new species "... differs from other species of carcharinus by having its mouth much broader, its first dorsal more anterior and its snout slightly shorter." Chen (1963), in a review of the sharks of Taiwan, identified *latistomus* as a junior synonym of *sorrah* but this is patently incorrect.

Although Whitley (1944) did not add luster to his record when he described *dorsalis* only from photographs of specimens from Western Australia, his account nevertheless can reasonably be interpreted as pertaining to *plumbeus*. The only illustration accompanying the account is a traced outline from a photograph showing a shark in an antero-oblique view. The prime diagnostic feature suggesting *plumbeus* is the very high first dorsal fin, with its origin apparently above the axil of the pectoral. Whitley stated that there was "Apparently no interdorsal ridge," but I doubt that this could be assessed from the photograph. The color was said to be "very light grey. No conspicuous dark marks on fins," and the length was up to about 5 ft (1,524 mm). Subsequently Whitley (1945) recorded *dorsalis* from other localities in Western Australia including Shark's Bay, Dirk Hartog Island, and well to the south off Bunbury. He accompanied these records with illustrations of a Dirk Hartog Island specimen which is obviously *plumbeus*, and he noted that an interdorsal ridge was present. Further support is available for accepting the presence of *plumbeus* in Australian waters from Whitley's (1964) account of two sharks (as *stevensi* Ogilby) from Swain Reefs, Queensland. Judging by differences in the position of the first dorsal origin relative to the pectoral fins, the two sharks were different species. The female from Gillett Cay, which was 6 ft 7 in (2,007 mm) long, was illustrated and described by Whitley and can fairly confidently be ascribed to *plumbeus*.

Description (see also Table 66).—Moderately large sharks growing to 2.4 m TL. Midline of back between dorsal fins with a low but well-marked dermal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles wide-spaced, not overlapping in small and half-grown specimens but more closely packed and partially overlapping in adults, rather large in size, ovoid, considerably wider than long, each with three longitudinal ridges and corresponding short posterior marginal teeth in embryos and juveniles, and with the same number or more usually five ridges and feeble, scarcely projecting teeth in adults.

Snout of moderate length and bluntly rounded in contour. Anterior margin of eye usually slightly forward of front of mouth but in some specimens it is above it. Nostrils strongly oblique, with rather broadly ovate apertures, the anterior margin of each nostril with a prominent nasal lobe.

Dental formula $\frac{14-1-14}{13-1-13}$ in 5 specimens out of 10 counted by me; 4 further specimens had $\frac{14-1-14}{14-1}$ or $\frac{14-1-14}{2-14}$ and the remaining one had $\frac{14-1-14}{13-1-14}$. Upper teeth broadly triangular, oblique except for the first series on each side of symphysis, their lateral margins concave along most of the row but notched on the outermost three or four series, their medial margins almost straight to weakly convex, both margins serrated, the serrations slightly coarser basally; one or occasionally two small symphyseal teeth. Lower teeth narrow, erect, with both margins very finely serrated, the serrations only on the distal halves of the cusps of the teeth towards the center of the mouth whereas towards the corners of the mouth the cusps are completely serrated; one or very occasionally two small symphyseal teeth.

First dorsal fin notably large, erect or slightly falcate, long based but narrow apically, very high in subadults and adults though much less so in small specimens (Fig. 63); origin of first dorsal over or slightly anterior to pectoral axil. Second dorsal fin moderately large and relatively high, similar to anal fin but lower and with a concave rather than notched distal margin; length of second dorsal rear tip 1.0-1.6 (mean 1.2) times second dorsal height for 16 specimens; origin of second dorsal about over anal fin origin. Pectoral fins rather large, long based, slightly or not falcate, their distal margins only weakly concave, their tips narrowly rounded; origin of pectorals a little anterior to fourth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches to as far as first dorsal axil in juveniles but half to two-thirds along first dorsal rear tip in sub-adults and adults.

Color in life was described by Wheeler (1963) from Mauritius-Seychelles specimens as "The colour on the back is palely blue—or greenish-grey and the lateral stripes from the origin of the pectoral towards the anus are faintly marked. The belly is white. D1 and D2 are coloured as the back but the posterior margins and extreme tips are blackish. The pectorals are dark grey on their dorsal surfaces, white ventrally with black trailing edges and slight grey or blackish tips. The dorsal lobe of the caudal is grey, the ventral lobe sometimes whitish. Both lobes have thin black posterior margins." After preservation in alcohol the color is gray or grayish brown above, pale to white below, usually with a faint indication of a horizontal tongue of the pale color extending forward part way along the side of the trunk from above the pelvic base. In juveniles, and in some adults, the apex of the second dorsal fin, the upper margin and tip of the dorsal lobe of the caudal fin, and the distal margin of the first dorsal fin are dusky edged.

Vertebral counts of eight specimens are given in Table 66 and of another seven specimens in Table 67. Counts for the Paris Museum syntype of *milberti* (MNHN 1142) are notably lower (P 82, C 70, T 152) than those in any other specimen reported. However, examination of the radiograph of this syntype indicates that its low counts are extreme due to diplospondyly occurring far rearward (at two-thirds of the distance from pelvic tips to anal fin origin) and the presence of several irregular groups of elongated centra amongst the shorter diplospondylous centra in both the precaudal and caudal regions. If the syntype counts are excluded, the range of counts for the remaining specimens are P 87-97, C 82-92, T 172-187. Not enough counts are available from different localities in the present sample to allow meaningful comparison between geographical regions. Despite this, some comparison can be made, as in Table 68, between 7 western North Atlantic specimens in the present sample (excluding the aberrant paratype of *milberti* which was from New York) and summarized counts of 26 specimens from Natal, South Africa, reported by Bass et al. (1973). These data give the western Indian Ocean material considerably higher total counts and slightly higher precaudal counts. The counts from two Mediterranean specimens (from Yugoslavia and Tunisia) agree more with the western Indian Ocean specimens, as might be expected, than with the western North Atlantic. The Yugoslavian specimen has a higher number of precaudals (97) than any other, though it is approached by Bass et al.'s (1973) upper count of 96.

Centrum diameter greater than centrum length except in last few monospondylous centra at posterior of abdomen which are almost square in profile or exceptionally have the centrum length greater. Diplospondyly occurs variously from above the pelvic axil to as far

Table 66.—*Carcharhinus plumbeus*, proportional dimensions in percentage of total length.

	♀ 390 mm Florida Englewood USNM 106547	♂ 522 mm Brazil Vitória SU 52846	♂ 530 mm Mexico Socorro Is. USNM 118395	♂ 586 mm Yugoslavia Spalato NMV (---)	♂ 598 mm New York New York MNHN 1142	♀ 666 mm Maryland Solomons Is. USNM 92404	♀ 1,207 mm Red Sea Rabigh NMV (---)	♀ 1,252 mm New Jersey New Jersey USNM 19667	♂ 1,445 mm Hawaiian Is. Oahu USNM 196594	♀ 1,670 mm Hawaiian Is. Oahu USNM 196599
Snout tip to										
outer nostrils	3.5	3.8	3.8	3.4	3.8	3.5	3.6	3.2	3.1	2.4
eye	7.5	7.7	7.2	7.5	7.9	7.4	7.2	6.7	6.8	5.6
mouth	8.1	8.0	7.5	7.5	7.8	7.8	7.4	7.2	7.2	5.6
1st gill opening	19.0	19.7	19.2	18.9	18.9	19.2	—	18.8	19.2	18.4
3d gill opening	21.5	22.4	21.5	21.1	21.7	21.9	—	21.2	21.2	21.1
5th gill opening	23.6	24.5	23.8	23.4	24.3	23.6	—	23.1	23.4	23.3
pectoral origin	22.6	23.8	22.4	22.6	23.6	22.8	22.6	21.7	22.3	21.3
pelvic origin	50.8	48.8	49.0	48.8	49.9	51.0	47.6	51.9	47.9	53.3
1st dorsal origin	29.0	28.9	29.4	29.4	28.9	28.2	28.1	28.6	28.0	28.4
2d dorsal origin	63.1	61.9	64.3	62.5	61.2	63.2	60.7	62.0	62.4	66.2
anal fin origin	62.1	61.9	62.3	62.0	61.9	63.0	60.7	63.3	62.6	66.2
upper caudal origin	75.4	73.8	75.4	74.0	74.0	75.4	72.9	73.9	73.9	77.9
lower caudal origin	74.6	73.0	74.5	72.7	72.9	74.8	71.7	73.8	73.1	77.3
Nostrils										
distance between inner corners	6.4	6.2	5.8	6.0	5.8	6.3	6.1	6.0	6.4	6.2
Mouth										
width	8.6	7.8	8.2	8.2	8.8	9.0	8.2	8.8	9.1	8.3
length	4.6	4.5	4.7	4.7	5.0	4.6	5.1	4.2	4.6	4.7
Labial furrow lengths										
upper	0.5	0.4	0.8	0.5	0.6	0.4	0.5	0.5	0.6	0.6
lower	0.5	0.4	0.5	0.5	0.7	0.5	0.6	0.6	0.6	0.5
Gill opening lengths										
1st	3.2	2.3	2.8	3.2	3.5	3.7	3.3	3.0	3.5	2.8
3d	3.3	2.4	2.8	3.1	3.7	3.7	3.6	3.4	3.3	3.1
5th	2.4	1.7	2.1	2.2	2.9	2.5	2.3	2.7	2.1	2.1
Eye										
horizontal diameter	2.9	2.3	2.5	2.3	2.4	2.3	1.8	1.9	1.7	1.8
1st dorsal fin										
length of base	12.8	11.1	11.1	11.1	11.4	12.8	11.3	12.2	12.2	13.8
length posterior margin	4.0	3.6	3.7	4.1	3.9	3.6	5.3	4.4	4.8	5.1
height	8.6	8.4	9.4	9.5	9.9	9.8	13.4	11.7	13.6	15.0
2d dorsal fin										
length of base	5.4	4.2	4.3	4.4	4.8	5.0	4.8	5.1	4.5	4.7
length posterior margin	3.3	3.3	3.2	3.3	3.3	3.0	3.4	3.4	3.7	3.8
height	2.6	2.7	2.6	2.8	3.3	2.7	3.0	3.0	2.8	3.3
Anal fin										
length of base	5.8	4.2	4.2	4.5	4.4	5.1	4.5	4.8	4.6	5.0
length posterior margin	3.5	3.2	3.4	3.2	3.2	2.8	3.5	3.5	3.6	3.5
height	3.3	3.5	3.8	3.3	4.1	3.2	3.5	3.6	3.6	4.3
Pectoral fin										
length of base	7.2	6.3	5.9	6.5	6.4	7.1	7.0	7.3	6.9	8.4
length anterior margin	16.9	17.8	17.0	16.9	16.9	16.9	22.1	20.0	21.7	22.4
length distal margin	8.5	11.3	11.9	12.5	13.4	11.9	17.3	16.1	18.4	19.1
greatest width	9.2	9.2	9.6	9.4	9.7	9.9	10.9	11.8	11.6	11.4
Pelvic fin										
length of base	5.3	4.9	5.7	5.1	5.7	5.3	5.8	5.0	6.0	6.0
length anterior margin	6.3	5.4	5.1	5.8	5.5	5.9	5.8	6.0	6.4	6.9
length distal margin	5.6	5.4	5.5	5.6	6.2	5.2	6.1	6.1	6.2	7.2
length of claspers	—	2.2	2.1	2.2	2.0	—	—	—	10.0	—
Caudal fin										
length of upper lobe	23.8	28.2	25.7	26.2	26.7	26.3	27.7	26.0	27.3	26.3
length of lower lobe	10.4	10.1	10.9	10.8	10.4	10.8	11.8	11.1	11.2	12.0
Trunk at pectoral origin										
width	13.1	12.1	12.5	11.1	12.0	13.2	—	13.2	13.8	—
height	13.1	10.3	10.2	10.8	10.1	11.9	—	11.2	12.1	—
Dental formula	—	—	14-1-14 13-1-13	14-1-14 13-1-13	14-1-14 13-1-14	14-1-14 14-1-14	—	—	14-1-14 13-1-13	14-2-14 14-1-14
Vertebrae										
precaudal	90	92	88	97	82	89	—	90	90	—
caudal	82	90	92	90	70	86	—	85	86	—
total	172	182	180	187	152	175	—	175	176	—

¹Syntype of *Carcharias* (*Prionodon*) *milberti*.

specimen a ridiculously small second dorsal. Similarly, under "Characteristics" of the species, *caudata* is said to be from 3 to 6 ft in length, yet the specimen described was given a length of 7 ft 4 in. Despite these careless errors, and the lack of type material, there is little doubt that De Kay was describing a specimen of *plumbeus*, and he himself notes that *caudata* is "... closely allied to the *C. ceruleus* = *plumbeus*] previously described."

The description of *japonicus* Temminck and Schlegel, 1850 provides very little information other than to note that the species is similar to "*Prionodon lamia* et *gangeticus*, et notamment avec la dernière espèce, mais dont elle s'éloigne par sa première dorsale beaucoup plus élevée et plus pointue." The size was stated rarely to exceed 6 ft (1,829 mm). The illustrations include a dorsal view of a whole shark (which appears to have an interdorsal ridge) and a lateral view of the tail. The latter is significant since it shows upper and lower precaudal pits typical of *Carcharhinus*, but excluding *gangeticus*. The dorsal view of the whole shark displays the first dorsal fin reflexed to one side, thus clearly portraying its shape, proportions, and position. In total the illustrations suggest *plumbeus* rather than any other species. This interpretation is reinforced to some extent by the type material of *japonicus* which comprises only two pairs of jaws, both of which I have seen in the Leiden Museum. One of these (RNH 334, cat.ost. b) with a dental formula of $\frac{1-14-2-14-1}{1-14-3-14-1}$ seems referable to *plumbeus*, as noted earlier by Hooijer (1954) who identified it as *milberti*. The other pair (RNH 335, cat. ost. a) were thought by Hooijer to come from *melanopterus* Quoy and Gaimard, but the dental formula $\left(\frac{16-3-15}{15-3-14}\right)$ excludes that species; instead this pair appears to be from *brachyurus* Günther.

Moreau (1881:332) described *obtusirostris* (inadvertently spelled *obtusirostris*) as a provisional replacement name for *lamia* of Risso pending clarification of the status of *longimanus* Poey. From this, and the references he cited including *lamia* of Müller and Henle, his intention to describe a white tip seems patently clear. However, his description, with one exception, gives no indication that he was dealing with white tips, but instead points fairly clearly to *plumbeus*. The exception is that he described the pectoral fins as "... deux fois au moins aussi longues que larges," and assuming that he measured the breadth of the pectoral in the same manner as Duméril (1865:355)—i.e., from pectoral origin to inner (posterior) corner, which is different from the method used in the present study, p. 4—this would agree with the white tip, *longimanus*, but not with *plumbeus*. I cannot reconcile this discrepancy, unless it means that Moreau had more than one species in his material or made an error of measurement, and hence I must disregard it in view of the weight of evidence supporting the interpretation of *obtusirostris* as *plumbeus*. Particular items which favor the latter are that the first dorsal fin was well forward, its origin being near the end of the pectoral base; the second dorsal fin was above the anal fin; the color was "brun cendré" and there was no mention of white markings on the fins; and the illustrations of the head and teeth. The illustrations show an obvious pointed lobe on each anterior nasal flap (such as in *plumbeus* where it is more developed than in *longimanus*) and upper teeth which better agree with those of *plumbeus* in their obliqueness and curvature than with those of *longimanus*. The number of upper teeth on each side was given as 12 or 14; neither *plumbeus* or *longimanus* have 12, but both can have 14. Finally, there is the fact that *plumbeus* is common in the Mediterranean, whereas there is no clear evidence that *longimanus* occurs there.

If the above interpretation of *obtusirostris* as a synonym of *plumbeus* is to be sustained, there is a need to explain why Moreau should have believed that they were separate species. The reason for Moreau's belief is not apparent from his 1881 account, for although he states there that *obtusirostris* and *milberti* (= *plumbeus*) differ in preoral length versus mouth width proportions, these differences do not stand up to scrutiny and in fact Moreau himself later reached the same conclusion as evidenced by a key in an account (1891) dealing principally with *milberti* but with some data on *obtusirostris*. In this key Moreau grouped *obtusirostris* with *milberti* in preoral length:mouth width proportions but separated them on pectoral length:breadth proportions. He emphasized this difference in his description of *milberti*—"cette différence dans les proportions des pectorales est peut-être le seul caractère qui permette de sûrement distinguer les jeunes de chacune des deux espèces"—and stated that in *milberti* pectoral breadth is almost five-sevenths of its length whereas in *obtusirostris* the pectoral length is at least twice its breadth. As evidence of the difference he gave measurements of three specimens, these being the Paris Museum syntype of *milberti* (male, 610 mm TL), an embryo of *milberti* (male, 410 mm), and an embryo of *obtusirostris* (male, 420 mm). From his measurements the values of pectoral $\frac{\text{length}}{\text{breadth}}$ are 1.44 and 1.65 for the syntype and embryo, respectively, of *milberti* and 2.1 for the embryo of *obtusirostris*, and thus in accord with his (Moreau 1891) description. However, I have examined what appear to be the two embryos which Moreau measured and which are now in the Paris Museum and I cannot confirm this difference in pectoral fin proportions nor do I find any other important difference. Both embryos are labelled as from France, Nice, Moreau; the *obtusirostris* specimen bears the number MNHN 98-1227, while the *milberti* specimen, along with another in the same jar, a female embryo of 400 mm, is MNHN 98-1229. Measurements of the *obtusirostris* embryo were kindly provided by Ch. Roux of the Paris Museum, and these show that, although pectoral length (70 mm) is the same as given by Moreau, pectoral width is 45 mm rather than 33 mm as given by Moreau, and hence pectoral $\frac{\text{length}}{\text{breadth}}$ is 1.56 instead of 2.1. Tortonese (1951b) had earlier examined the same embryos and illustrated the *obtusirostris* (MNHN 98-1227). His illustration likewise shows pectoral $\frac{\text{length}}{\text{breadth}}$ as about 1.5. This value for pectoral $\frac{\text{length}}{\text{breadth}}$ of *obtusirostris* is, therefore, within the range which Moreau himself gave for *milberti*.

The above findings cast doubt on the primary diagnostic feature used by Moreau to separate *obtusirostris* and *milberti* and lend weight to the view that these species are conspecific. However, the findings cannot be interpreted as simply as this, even though there is little doubt that, firstly, *obtusirostris* as described and illustrated by Moreau (1881) seems mainly referable to *plumbeus* and, secondly, that the embryos of *obtusirostris* and *milberti* for which Moreau (1891) gave measurements are not different species. The need for caution in interpretation is because these latter embryos are not specimens of *plumbeus* but instead are *brachyurus* Günther. Although embryos are frequently more difficult to identify than free-living specimens, my identification of Moreau's embryos as *brachyurus* was

able to be made before other evidence became available to confirm that *brachyurus* is present in the Mediterranean. Subsequent analysis of data on proportional dimensions shows that the measurements given by Moreau (1891) for his embryos point clearly to both of them being *brachyurus*. In particular, the length of the first dorsal base separates *brachyurus* from *plumbeus* as indicated in Table 65 where Moreau's measurements are also given for comparison.

Table 65.—Length of first dorsal fin base as percentage of total length in *Carcharhinus brachyurus* and *C. plumbeus*, and comparable data from Moreau's (1891) account of *C. obtusirostris* and *C. milberti*.

	Data from present study		Data from Moreau (1891)		
	<i>brachyurus</i> 16 specimens 650-2,725 mm TL	<i>plumbeus</i> 15 specimens 390-1,670 mm TL	" <i>obtusirostris</i> " 1 embryo 420 mm TL	" <i>milberti</i> " 1 embryo 410 mm TL	" <i>milberti</i> " New York syntype 610 mm TL
First dorsal base as % TL					
Range (mean)	8.9-10.8 (9.7)	11.1-13.8 (11.9)	9.5	8.8	11.1

A further complication is presented by Moreau's (1891) description of *milberti*. The description is based partly on the New York syntype of *milberti* and partly on other specimens which, except for the embryo discussed above, are not itemized other than in terms of their general size, e.g., "très-grande taille, moyenne taille, adultes, jeunes," etc. Judging by Moreau's illustrations of the teeth (his figures 221 and 222, and especially the latter) and the dental formula he gave $\frac{15-1-15}{15-1-15}$, there is no doubt that some of these other specimens and perhaps all of them were *brachyurus* rather than *milberti*. This misidentification which Moreau made provides the clue needed for understanding why he should have described *obtusirostris* as a species separate from *milberti* (*plumbeus*). He did so because, in general, his *milberti* equals *brachyurus* and his *obtusirostris* equals *plumbeus*. This interpretation is satisfactory but it raises one nomenclatural difficulty. Compagno (1973b) listed as holotype of *obtusirostris* the 420 mm male embryo (MNHN 98-1227) for which Moreau (1891) gave measurements, thus more firmly categorizing its status than did Tortonese (1951b) who presumed it was the type. However, if this designation were accepted it would make *obtusirostris* a junior synonym of *brachyurus*, which is at variance with Moreau's (1881) account in which he was clearly, if not exclusively, dealing with *plumbeus*. The situation can best be met by disregarding Compagno's listing on the grounds that there is no definite evidence to establish that MNHN 98-1227 is either a holotype or type material at all. Moreau (1881) did not list the specimen, although it may have been the "jeune individu" he mentioned in the description. Ch. Roux informs me that MNHN 98-1227 was catalogued in 1898 along with the rest of Moreau's collections which were given to the museum following his death in 1896. Catalogue data do not show when the specimen was collected. It is conceivable that it was not collected until after 1881 along with the other similar-sized embryos (MNHN 98-1228, 98-1229) which Moreau treated as *milberti* and one of which he listed along with MNHN 98-1227 in 1891. It is clear from Moreau's (1881) text on *milberti* that he did not have these "*milberti*" embryos at that time.

Ogilby's (1911:38) description of *stevensi*, based on two specimens from Queensland, Australia, was not illustrated, and the type material originally held in the Queensland Museum appears to have been lost according to McCulloch in Whitley (1934) who also noted that the lengths of the two specimens (164 and 187 cm) were erroneously given in millimeters rather than centimeters. A further oversight by Ogilby was in heading his description on page 38 as "*Carcharias stevensi*" rather than as "*Carcharhinus stevensi*." That he intended the latter is evident in his introduction on page 36. The description, which is reasonably good and includes many proportional measurements, has been variously interpreted by later authors. For example, Whitley's (1940) account of *stevensi* is referable to *leucas* whereas his 1943 interpretation appears to be *obscurus* and his 1964 descriptions apply to *plumbeus* (Gillett Cay specimen) and some other species (Capre Cay specimen).

Ogilby (1911) regarded *stevensi* as distinctive in the "... extreme shortness of the postventral portion of the body ..." but I do not find this to be a very useful diagnostic character. A more important item in the description is the vertical height of the first dorsal fin. Ogilby gave this as 1.25-1.33 in the length of head, and the latter as 4.9 in the total length; if these proportions are converted, then the first dorsal height ranged from 15.3 to 16.3% TL. From figure 5 it can be seen that the only two species which have or approach these high values are *plumbeus* and *longimanus*. The latter can be discounted in terms of its color pattern, the shape of the first dorsal fin apex, and in some proportional dimensions. On the other hand, agreement between *plumbeus* and *stevensi* is, in general, very good, and this, coupled with the fact that *plumbeus* occurs in Queensland waters, is sufficient to leave little doubt that they are conspecific. The chief disquieting feature at first glance is Ogilby's statement that in *stevensi* the eye is "... inserted midway between the tip of the snout and the second gill-opening. ..." However, apart from this not occurring in any species of *Carcharhinus* the statement does not agree with another item in the description that the snout length (i.e., preocular) is "... 1.7 in the space between the eye and the first gill-opening. ..." This latter item is perfectly feasible for *plumbeus* but obviously would not permit the eye to be anywhere near to midway between snout tip and second gill opening. Other minor differences between *stevensi* and *plumbeus* are in the description of the lower teeth. Firstly, the number of 15-0-15 is improbable for *plumbeus* but could be explained by Ogilby counting symphysial teeth as laterals—on this basis a formula of 14-2-14 is possible. Secondly, the lower teeth were described as "entire" (i.e., smooth edged) but this may only mean that their fine serrations were overlooked.

Fang and Wang's (1932) account of *latistomus* as a new species from China agrees well enough with *plumbeus* for me to refer it to that species, although the description is rather general and no dental formula or illustration of the teeth is given. The account, including two illustrations, was based only on the holotype, a juvenile of "... 565 mm. to last vertebra," deposited as No. 11156 in the Museum of the Biological Laboratory of the Science Society of China; I do not know if this holotype is still in existence. The only diagnostic

comparison made by Fang and Wang was to state that their new species "... differs from other species of *carcharinus* by having its mouth much broader, its first dorsal more anterior and its snout slightly shorter." Chen (1963), in a review of the sharks of Taiwan, identified *latistomus* as a junior synonym of *sorrah* but this is patently incorrect.

Although Whitley (1944) did not add luster to his record when he described *dorsalis* only from photographs of specimens from Western Australia, his account nevertheless can reasonably be interpreted as pertaining to *plumbeus*. The only illustration accompanying the account is a traced outline from a photograph showing a shark in an antero-oblique view. The prime diagnostic feature suggesting *plumbeus* is the very high first dorsal fin, with its origin apparently above the axil of the pectoral. Whitley stated that there was "Apparently no interdorsal ridge," but I doubt that this could be assessed from the photograph. The color was said to be "very light grey. No conspicuous dark marks on fins," and the length was up to about 5 ft (1,524 mm). Subsequently Whitley (1945) recorded *dorsalis* from other localities in Western Australia including Shark's Bay, Dirk Hartog Island, and well to the south off Bunbury. He accompanied these records with illustrations of a Dirk Hartog Island specimen which is obviously *plumbeus*, and he noted that an interdorsal ridge was present. Further support is available for accepting the presence of *plumbeus* in Australian waters from Whitley's (1964) account of two sharks (as *stevensi* Ogilby) from Swain Reefs, Queensland. Judging by differences in the position of the first dorsal origin relative to the pectoral fins, the two sharks were different species. The female from Gillett Cay, which was 6 ft 7 in (2,007 mm) long, was illustrated and described by Whitley and can fairly confidently be ascribed to *plumbeus*.

Description (see also Table 66).—Moderately large sharks growing to 2.4 m TL. Midline of back between dorsal fins with a low but well-marked dermal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles wide-spaced, not overlapping in small and half-grown specimens but more closely packed and partially overlapping in adults, rather large in size, ovoid, considerably wider than long, each with three longitudinal ridges and corresponding short posterior marginal teeth in embryos and juveniles, and with the same number or more usually five ridges and feeble, scarcely projecting teeth in adults.

Snout of moderate length and bluntly rounded in contour. Anterior margin of eye usually slightly forward of front of mouth but in some specimens it is above it. Nostrils strongly oblique, with rather broadly ovate apertures, the anterior margin of each nostril with a prominent nasal lobe.

Dental formula $\frac{14-1-14}{13-1-13}$ in 5 specimens out of 10 counted by me; 4 further specimens had $\frac{14-1-14}{14-1}$ or $\frac{14-1-14}{2-14}$ and the remaining one had $\frac{14-1-14}{13-1-14}$ Upper teeth broadly triangular, oblique except for the first series on each side of symphysis, their lateral margins concave along most of the row but notched on the outermost three or four series, their medial margins almost straight to weakly convex, both margins serrated, the serrations slightly coarser basally; one or occasionally two small symphyseal teeth. Lower teeth narrow, erect, with both margins very finely serrated, the serrations only on the distal halves of the cusps of the teeth towards the center of the mouth whereas towards the corners of the mouth the cusps are completely serrated; one or very occasionally two small symphyseal teeth.

First dorsal fin notably large, erect or slightly falcate, long based but narrow apically, very high in subadults and adults though much less so in small specimens (Fig. 63); origin of first dorsal over or slightly anterior to pectoral axil. Second dorsal fin moderately large and relatively high, similar to anal fin but lower and with a concave rather than notched distal margin; length of second dorsal rear tip 1.0-1.6 (mean 1.2) times second dorsal height for 16 specimens; origin of second dorsal about over anal fin origin. Pectoral fins rather large, long based, slightly or not falcate, their distal margins only weakly concave, their tips narrowly rounded; origin of pectorals a little anterior to fourth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches to as far as first dorsal axil in juveniles but half to two-thirds along first dorsal rear tip in sub-adults and adults.

Color in life was described by Wheeler (1963) from Mauritius-Seychelles specimens as "The colour on the back is palely blue—or greenish-grey and the lateral stripes from the origin of the pectoral towards the anus are faintly marked. The belly is white. D1 and DII are coloured as the back but the posterior margins and extreme tips are blackish. The pectorals are dark grey on their dorsal surfaces, white ventrally with black trailing edges and slight grey or blackish tips. The dorsal lobe of the caudal is grey, the ventral lobe sometimes whitish. Both lobes have thin black posterior margins." After preservation in alcohol the color is gray or grayish brown above, pale to white below, usually with a faint indication of a horizontal tongue of the pale color extending forward part way along the side of the trunk from above the pelvic base. In juveniles, and in some adults, the apex of the second dorsal fin, the upper margin and tip of the dorsal lobe of the caudal fin, and the distal margin of the first dorsal fin are dusky edged.

Vertebral counts of eight specimens are given in Table 66 and of another seven specimens in Table 67. Counts for the Paris Museum syntype of *milberti* (MNHN 1142) are notably lower (P 82, C 70, T 152) than those in any other specimen reported. However, examination of the radiograph of this syntype indicates that its low counts are extreme due to diplospondyly occurring far rearward (at two-thirds of the distance from pelvic tips to anal fin origin) and the presence of several irregular groups of elongated centra amongst the shorter diplospondylous centra in both the precaudal and caudal regions. If the syntype counts are excluded, the range of counts for the remaining specimens are P 87-97, C 82-92, T 172-187. Not enough counts are available from different localities in the present sample to allow meaningful comparison between geographical regions. Despite this, some comparison can be made, as in Table 68, between 7 western North Atlantic specimens in the present sample (excluding the aberrant paratype of *milberti* which was from New York) and summarized counts of 26 specimens from Natal, South Africa, reported by Bass et al. (1973). These data give the western Indian Ocean material considerably higher total counts and slightly higher precaudal counts. The counts from two Mediterranean specimens (from Yugoslavia and Tunisia) agree more with the western Indian Ocean specimens, as might be expected, than with the western North Atlantic. The Yugoslavian specimen has a higher number of precaudals (97) than any other, though it is approached by Bass et al.'s (1973) upper count of 96.

Centrum diameter greater than centrum length except in last few monospondylous centra at posterior of abdomen which are almost square in profile or exceptionally have the centrum length greater. Diplospondyly occurs variously from above the pelvic axil to as far

Table 66.—*Carcharhinus plumbeus*, proportional dimensions in percentage of total length.

	♀ 390 mm Florida Englewood USNM 106547	♂ 522 mm Brazil Vitória SU 52846	♂ 530 mm Mexico Socorro Is. USNM 118395	♂ 586 mm Yugoslavia Spalato NMV (---)	♂ 598 mm New York MNHN 1142	♀ 666 mm Maryland Solomons Is. USNM 92404	♀ 1,207 mm Red Sea Rabigh NMV (---)	♀ 1,252 mm New Jersey USNM 19667	♂ 1,445 mm Hawaiian Is. USNM 196594	♀ 1,670 mm Hawaiian Is. USNM 196599
Snout tip to										
outer nostrils	3.5	3.8	3.8	3.4	3.8	3.5	3.6	3.2	3.1	2.4
eye	7.5	7.7	7.2	7.5	7.9	7.4	7.2	6.7	6.8	5.6
mouth	8.1	8.0	7.5	7.5	7.8	7.8	7.4	7.2	7.2	5.6
1st gill opening	19.0	19.7	19.2	18.9	18.9	19.2	—	18.8	19.2	18.4
3d gill opening	21.5	22.4	21.5	21.1	21.7	21.9	—	21.2	21.2	21.1
5th gill opening	23.6	24.5	23.8	23.4	24.3	23.6	—	23.1	23.4	23.3
pectoral origin	22.6	23.8	22.4	22.6	23.6	22.8	22.6	21.7	22.3	21.3
pelvic origin	50.8	48.8	49.0	48.8	49.9	51.0	47.6	51.9	47.9	53.3
1st dorsal origin	29.0	28.9	29.4	29.4	28.9	28.2	28.1	28.6	28.0	28.4
2d dorsal origin	63.1	61.9	64.3	62.5	61.2	63.2	60.7	62.0	62.4	66.2
anal fin origin	62.1	61.9	62.3	62.0	61.9	63.0	60.7	63.3	62.6	66.2
upper caudal origin	75.4	73.8	75.4	74.0	74.0	75.4	72.9	73.9	73.9	77.9
lower caudal origin	74.6	73.0	74.5	72.7	72.9	74.8	71.7	73.8	73.1	77.3
Nostrils										
distance between inner corners	6.4	6.2	5.8	6.0	5.8	6.3	6.1	6.0	6.4	6.2
Mouth										
width	8.6	7.8	8.2	8.2	8.8	9.0	8.2	8.8	9.1	8.3
length	4.6	4.5	4.7	4.7	5.0	4.6	5.1	4.2	4.6	4.7
Labial furrow lengths										
upper	0.5	0.4	0.8	0.5	0.6	0.4	0.5	0.5	0.6	0.6
lower	0.5	0.4	0.5	0.5	0.7	0.5	0.6	0.6	0.6	0.5
Gill opening lengths										
1st	3.2	2.3	2.8	3.2	3.5	3.7	3.3	3.0	3.5	2.8
3d	3.3	2.4	2.8	3.1	3.7	3.7	3.6	3.4	3.3	3.1
5th	2.4	1.7	2.1	2.2	2.9	2.5	2.3	2.7	2.1	2.1
Eye										
horizontal diameter	2.9	2.3	2.5	2.3	2.4	2.3	1.8	1.9	1.7	1.8
1st dorsal fin										
length of base	12.8	11.1	11.1	11.1	11.4	12.8	11.3	12.2	12.2	13.8
length posterior margin	4.0	3.6	3.7	4.1	3.9	3.6	5.3	4.4	4.8	5.1
height	8.6	8.4	9.4	9.5	9.9	9.8	13.4	11.7	13.6	15.0
2d dorsal fin										
length of base	5.4	4.2	4.3	4.4	4.8	5.0	4.8	5.1	4.5	4.7
length posterior margin	3.3	3.3	3.2	3.3	3.3	3.0	3.4	3.4	3.7	3.8
height	2.6	2.7	2.6	2.8	3.3	2.7	3.0	3.0	2.8	3.3
Anal fin										
length of base	5.8	4.2	4.2	4.5	4.4	5.1	4.5	4.8	4.6	5.0
length posterior margin	3.5	3.2	3.4	3.2	3.2	2.8	3.5	3.5	3.6	3.5
height	3.3	3.5	3.8	3.3	4.1	3.2	3.5	3.6	3.6	4.3
Pectoral fin										
length of base	7.2	6.3	5.9	6.5	6.4	7.1	7.0	7.3	6.9	8.4
length anterior margin	16.9	17.8	17.0	16.9	16.9	16.9	22.1	20.0	21.7	22.4
length distal margin	8.5	11.3	11.9	12.5	13.4	11.9	17.3	16.1	18.4	19.1
greatest width	9.2	9.2	9.6	9.4	9.7	9.9	10.9	11.8	11.6	11.4
Pelvic fin										
length of base	5.3	4.9	5.7	5.1	5.7	5.3	5.8	5.0	6.0	6.0
length anterior margin	6.3	5.4	5.1	5.8	5.5	5.9	5.8	6.0	6.4	6.9
length distal margin	5.6	5.4	5.5	5.6	6.2	5.2	6.1	6.1	6.2	7.2
length of claspers	—	2.2	2.1	2.2	2.0	—	—	—	10.0	—
Caudal fin										
length of upper lobe	23.8	28.2	25.7	26.2	26.7	26.3	27.7	26.0	27.3	26.3
length of lower lobe	10.4	10.1	10.9	10.8	10.4	10.8	11.8	11.1	11.2	12.0
Trunk at pectoral origin										
width	13.1	12.1	12.5	11.1	12.0	13.2	—	13.2	13.8	—
height	13.1	10.3	10.2	10.8	10.1	11.9	—	11.2	12.1	—
Dental formula	—	—	14-1-14 13-1-13	14-1-14 13-1-13	14-1-14 13-1-14	14-1-14 14-1-14	—	—	14-1-14 13-1-13	14-2-14 14-1-14
Vertebrae										
precaudal	90	92	88	97	82	89	—	90	90	—
caudal	82	90	92	90	70	86	—	85	86	—
total	172	182	180	187	152	175	—	175	176	—

† Syntype of *Carcharias (Prionodon) milberti*.

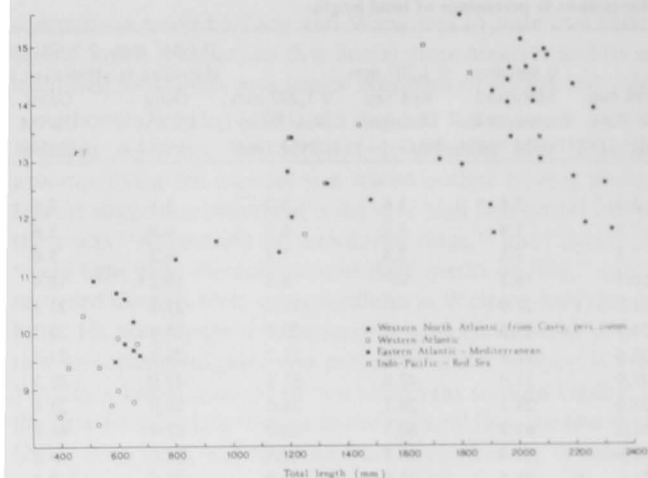


Figure 63.—First dorsal fin height as percent of total length versus total length in *Carcharhinus plumbeus*.

Table 67.—Vertebral numbers in seven specimens of *Carcharhinus plumbeus*.

Specimens		Precaudal	Caudal	Total
USNM 33334	Connecticut	88	86	174
USNM 117802	New York	87	88	175
USNM 195831	Maryland	91	84	175
USNM 187785	South Carolina	90	88	178
USNM 118395	Revillagigedo Is.	87	88	175
USNM 196596	Hawaii	94	88	182
—	Tunisia ¹	91	91	182
Range (including counts from Table 66)		82-97	70-92	152-187

¹Data from Quignard and Capapé (1971b).

Table 68.—Precaudal vertebral numbers in *Carcharhinus plumbeus* from the western North Atlantic and from Natal, South Africa.

Locality	Precaudal		Total		n
	Range	Mean	Range	Mean	
Western North Atlantic	87-91	89.3	172-178	174.8	7
Natal, South Africa	89-96	92.4	177-189	183.3	26

Table 69.—Number of embryos per litter, size at birth, size of mature specimens, and maximum size of *Carcharhinus plumbeus*.

	No. of embryos per litter			Size at birth (TL mm)	Smallest mature specimen (TL mm)		Largest specimen (TL mm)	
	Range	Mean	n		♂	♀	♂	♀
Western North Atlantic								
Southeastern U.S.A. (Springer 1960)	1-14	9.0	65	610-635	1,800	1,830	2,260	2,340
Florida (Clark and von Schmidt 1965)	4-12	9.0	26	—	1,920	1,850	2,040	2,300
Indian Ocean and Red Sea								
Southeastern Africa (Bass et al. 1973)	8	8.0	2	600-650	1,630	1,730	1,880	1,950
Madagascar (Fourmanoir 1961)	—	—	—	—	—	1,750	—	—
Mauritius-Seychelles (Wheeler 1963)	6-11	8.3	7	—	1,800	1,770	2,130	2,200
Red Sea (Baranes and Ben-Tuvia 1978)	6	6.0	1	—	—	1,764	—	—
Pacific Ocean								
East China Sea (Taniuchi 1971)	2-10	6.0	91	650-750	—	—	—	—
Hawaiian Islands (Tester see text footnote 4)	1-8	5.5	91	—	—	—	2,400-2,490 (sex not stated)	—
Hawaiian Islands (Wass in Bass et al. 1973)	—	—	—	—	1,310	1,440	1,730	1,910

back as the posterior tips of the pelvic fins in 9 of the 14 specimens radiographed, while in the other 5 it is farther rearward, ranging from just behind the pelvic tips to about two-thirds of the distance between them and the anal fin origin. Centra usually regular though in some of the specimens there is a distinct alternation in length of the diplospondylous centra along the caudal peduncle and the caudal fin axis, and there may also be one or more groups of slightly elongated centra usually at about the level of the second dorsal fin but sometimes farther rearward and on the caudal axis as well. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.87-1.03 (mean 0.95) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.52-1.82 (mean 1.70) in 13 specimens.

Published data on the number of embryos per litter, size at birth and at maturity, and maximum size of *plumbeus* are more extensive than for most other species of *Carcharhinus* and indicate considerable geographic variation (Table 69). Without exception the few observations made in the present study lie well within the ranges of values shown in Table 69. It can be seen that Hawaiian specimens

stand out from the others in having fewer embryos per litter, in maturing at a smaller size, and probably also in attaining a smaller maximum size (the 2,400-2,490 mm specimen listed by Tester (see footnote 4) was exceptional, for of 244 other specimens that he records the next largest were only in the range 1,800-1,890 mm). East China Sea material reported by Taniuchi (1971) is comparable with the Hawaiian material in number of embryos per litter, but there are no data for comparison of size at maturity or maximum size.

Distribution (see also Material examined).—*Carcharhinus plumbeus* is an abundant tropical-subtropical species with a wide distribution in coastal waters of the Atlantic, Mediterranean, Indian, and Pacific Oceans. However, except for the western North Atlantic where its range has been documented in detail by Bigelow and Schroeder (1948) and Springer (1960), knowledge of its distribution throughout other oceans is still for the most part sparse. Material which I have examined, supplemented by literature accounts (mostly of *milberti*) which leave no doubt of the identity of the species, give it a distribution as follows:

- 1) Western Atlantic from northeastern U.S.A. (Massachusetts) to southern Brazil (Cananéia) where it was recently recorded by Sadowsky (1967a). Within that range it is known to be common off most of the east coast of the U.S.A., but uncommon in the western Gulf of Mexico and along Central America (Springer 1960). It is seemingly uncommon also in the Caribbean although it is reported from Cuba (Guitart-Manday 1968) and from Venezuela (Cervigon 1966). Apart from meager data from the southern half of Brazil, information is lacking for the western South Atlantic.
- 2) Eastern Atlantic from southern Morocco (Agadir) and Senegal (Cadenat 1950) in the north, and from off the Congo (Poll 1951) at lat. 5°29'–5°57' S (Moanda and Banana). I cannot confirm other nominal listings from the eastern Atlantic, including the Canary Islands, but it is nevertheless, likely that *plumbeus* will be found to have a much longer eastern Atlantic range.
- 3) Mediterranean, particularly from the western half and from the Adriatic Sea (type locality). Undoubted records, which are unlikely to reflect in full its probably wider distribution in the area, include the southern coast of Spain (Rey 1928), Tunisia (Quignard and Capapé 1971a, b), both coasts of Italy, and Yugoslavia.
- 4) Red Sea from Koseir and Rabigh, and from Di-Zahav and Ras Muhammad (Baranes and Ben-Tuvia 1978).
- 5) Western Indian Ocean from the Gulf of Oman (Muscat) in the north, from the Seychelles (Wheeler 1953, as *bleekeri*), Mauritius-Seychelles area (Wheeler 1963, as *milberti*), Madagascar (Fourmanoir 1961, as *platyodon*), and from the east coast of central Africa to as far south as Natal where it has been well documented by Bass et al. (1973).
- 6) Eastern Indian Ocean from only Indonesia (Aru Islands) and from Western Australia at Carnarvon, Shark's Bay and Bunbury (Whitley 1944, 1945, as *dorsalis*).
- 7) Western Pacific from Japan (Nagasaki), China (Fukien and Ningpo), and the East China Sea where Taniuchi (1971) reported it as one of the most abundant sharks, and from off Queensland, Australia (Gillett Cay specimen as *stevensi* in Whitley 1964).
- 8) Central Pacific at the Hawaiian Islands where records by Tester (see footnote 4) showed it similarly to be the most abundant inshore shark.
- 9) Eastern Pacific where its presence is yet to be confirmed, though two newborn specimens (USNM 118395) taken by the *Albatross* in 1888 from the Revillagigedo Islands appear to be *plumbeus*, and Kato et al. (1967) listed it as possibly present at the Galapagos.

Material examined.—IFAN 56-889 - 56-893, seven embryos, four females, 300-350 mm, and three males, 320-330 mm, Senegal, Zoal, 5 December 1956, F. Paraiso; IFAN 56-885 - 56-888, six embryos, three females, 315-345 mm, and three males, 325-350 mm, Senegal, Zoal, 30 November 1956; MNHN 7659, two female embryos, 325 and 335 mm, Senegal, Gorée; USNM 106547, female embryo, 390 mm, Florida, Englewood, 20 January 1938, Bass Biological Laboratory; SMNS 3593, female embryo, 412 mm, Red Sea, Koseir, Klunzinger, 1894; USNM 196596, female embryo, 425 mm, Hawaiian Islands, Oahu, 1961, Hawaiian Fish and Game; ZSZM (uncat), male, 440 mm, and female, 445 mm, China, Fukien, 25 August 1905, G. Siemssen; USNM 125761, female embryo, 452 mm, Virginia, Ocean View, 18 October 1922, W. C. Schroeder; RNH 7381, female embryo, 477 mm, Indonesia, Aru Islands, P. Bleeker; BMNH 57.11.28.89, female embryo, 482 mm, no locality, Bleeker; ISZZ 4467, male, 510 mm [probable syntype of *Carcharias (Prionodon) milberti*], Italy, Trieste, Hemprich and Ehrenberg; SU 52846, male embryo, 522 mm, Brazil, Espirito Santo, Vitória, 13 December 1944; USNM 118395, two males, 530 and 590 mm, Mexico, Revillagigedo Islands, Socorro Island, March-April 1888, *Albatross*; IFAN 56-149, male embryo, 550 mm, Senegal, Zoal, 16 April 1956, J. Cadenat; USNM 83597, female embryo, 550 mm, Washington, D.C., Fish Market, 1919, E. D. Reid; USNM 195831, three males, 550-630 mm, and one female, 596 mm, Maryland, Chesapeake Bay, 21 July 1958, F. Schwartz; USNM 117802, male, 565 mm, New York, Long Island, 1901, T. H. Bean; IFAN 56-146 - 55-147, two embryos, female, 565 mm, and male, 570 mm, Senegal, Zoal, 16 April 1956, J. Cadenat; USNM 33334, male embryo, 572 mm, Connecticut, Branford, E. R. Kelsey; NMV 22415 (old no.), male, 586 mm, Yugoslavia, Spalato, April 1895; MNHN 1142, male, 598 mm [syntype of *Carcharias (Prionodon) milberti*], coast of New York, Milbert; NMV 61-384, male, 610 mm, China, Ningpo; ISZZ (uncat.) male, 620 mm, Massachusetts, Woods Hole; USNM 187785, male, 623 mm, off South Carolina, 33°38'N, 78°23'W, 13 December 1961, *Silver Bay*; USNM 89256, female, 650 mm, Washington, D.C., Fish Market, 28 September 1928; BMNH 79.10.9.4, male, 662 mm, Massachusetts, Woods Hole; USNM 92404, female, 666 mm, Maryland, Solomons Island, 13 September 1932, B. Babasham; IRSN 8.407, female, 677 mm, west Africa, off Moanda, 5°50'S, 12°03'E, 23 March 1949; IRSN 8.406, female, ca. 730 mm, west Africa, WNW of Banana, 5°29'S, 12°E, 25-26 September 1948, *M'Bizi*; USNM 104969, male, 750 mm, Chesapeake Bay, 26 August 1934, R. Taylor; MRAC 80262, female, ca. 800 mm, west Africa, WNW of Banana, 5°57'S, 12°E, 25 May 1948; NMV 61-428, female, 940 mm, Morocco, Agadir, 1904, Pietschmann; BMNH 88.12.29, mounted skin of male, ca. 940 mm, Gulf of Oman, Muscat, A. S. G. Jayarakar; USNM 125882, male, ca. 1,130 mm, Florida, Apalachicola Bay, 18 June 1932, I. Ginsburg; NMV (uncat.), female, 1,207 mm, Red Sea, Rabigh; USNM 196667, female, 1,252 mm, off New Jersey, 39°41'N, 73°48'W, 25 August 1961, V. G. Springer; USNM 196594, mature male, 1,445 mm, Hawaiian Islands, Oahu, off Kewalo Basin, September 1961, Hawaiian Fish and Game; RNH 2555, female, 1,540 mm [supposed syntype of *Carcharias (Prionodon) milberti*], Italy, Livorno; USNM 196599, female, 1,670 mm (discarded except for jaws), Hawaiian Islands, Oahu, off Kewalo Basin, August 1961.

Also USNM 7735, head and skin of juvenile, from New Jersey, Beesleys Point, S. F. Baird; SMF 2766, mounted skin from Italy, Messina, 1845, E. Rüppell; UZMK PO 689, specimen from Japan, Nagasaki, D. S. Jordan.

Also jaws at many institutions (especially IFAN), and including RNH 334, cat. ost. b [syntype of *Carcharias (Prionodon) japonicus*], Japan, D. W. Burger.

Carcharhinus altimus (Springer, 1950)
Figures 64, 65

Eulamia altima Springer, 1950:9-12. Immature female, 1,320 mm, Florida Keys.
Carcharinus radamae Fourmanoir, 1961:24-26, pls. 6, 7, text figs. 14-17, 1 table. Four adult females, 2,340, 2,540, 2,600, and 2,770 mm, off west coast of Madagascar.

Diagnosis.—Large sharks, up to 2.82 m long, with a low, broad interdorsal ridge; tips of fins, except the pelvic, somewhat dusky, more so in young than in adults; snout long and bluntly pointed to rounded; internarial width 1.3-1.4 in preoral length; origin of first dorsal fin over pectoral axil or behind it to almost as far back as halfway along inner pectoral margin; apex of first dorsal bluntly pointed; origin of second dorsal in front of anal fin origin; height of second dorsal 2.8-3.4% TL and 1.1-1.4 in length of its rear tip; dental formula usually $\frac{15-1-15}{14 \text{ or } 15-1-14 \text{ or } 15}$ but may be $\frac{14 \text{ to } 16-1 \text{ or } 2-14 \text{ to } 16}{14 \text{ or } 15-1-14 \text{ or } 15}$; upper teeth broad, noticeably long, oblique, and uniformly serrated; lower teeth erect, serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 101-110; caudal centra 94-96; total centra 194-206; diplospondyly begins one-third along pelvic base; diplospondylous centra regular in length; penultimate monospondylous centrum 1.5 times wider than long.

The noticeably long upper teeth and the prominent nasal lobe are important details in which *altimus* differs from the three other species, *galapagensis*, *obscurus*, and *plumbeus*, with which it might be confused. It shares with these three the presence of an interdorsal ridge, broad upper teeth, and no conspicuous color pattern. Other than by upper teeth shape and nasal lobe it is not readily separated from these three as a group, although on average it has a longer snout region and a longer first dorsal rear tip. It agrees with *plumbeus* but differs from *galapagensis* and *obscurus* in having the first dorsal origin over the pectoral axil or at least nearer to it than to the pectoral inner corner. In its precaudal vertebral numbers (101-110) it is separable from both *plumbeus* (82-97) and *obscurus* (86-97). It further differs from *obscurus* in its higher second dorsal fin (2.8-3.4% TL versus 1.5-2.3% in *obscurus*) and its lower ratio for the relationship second dorsal rear tip:second dorsal height (1.1-1.4 in *altimus*, 1.6-2.1 in *obscurus*).

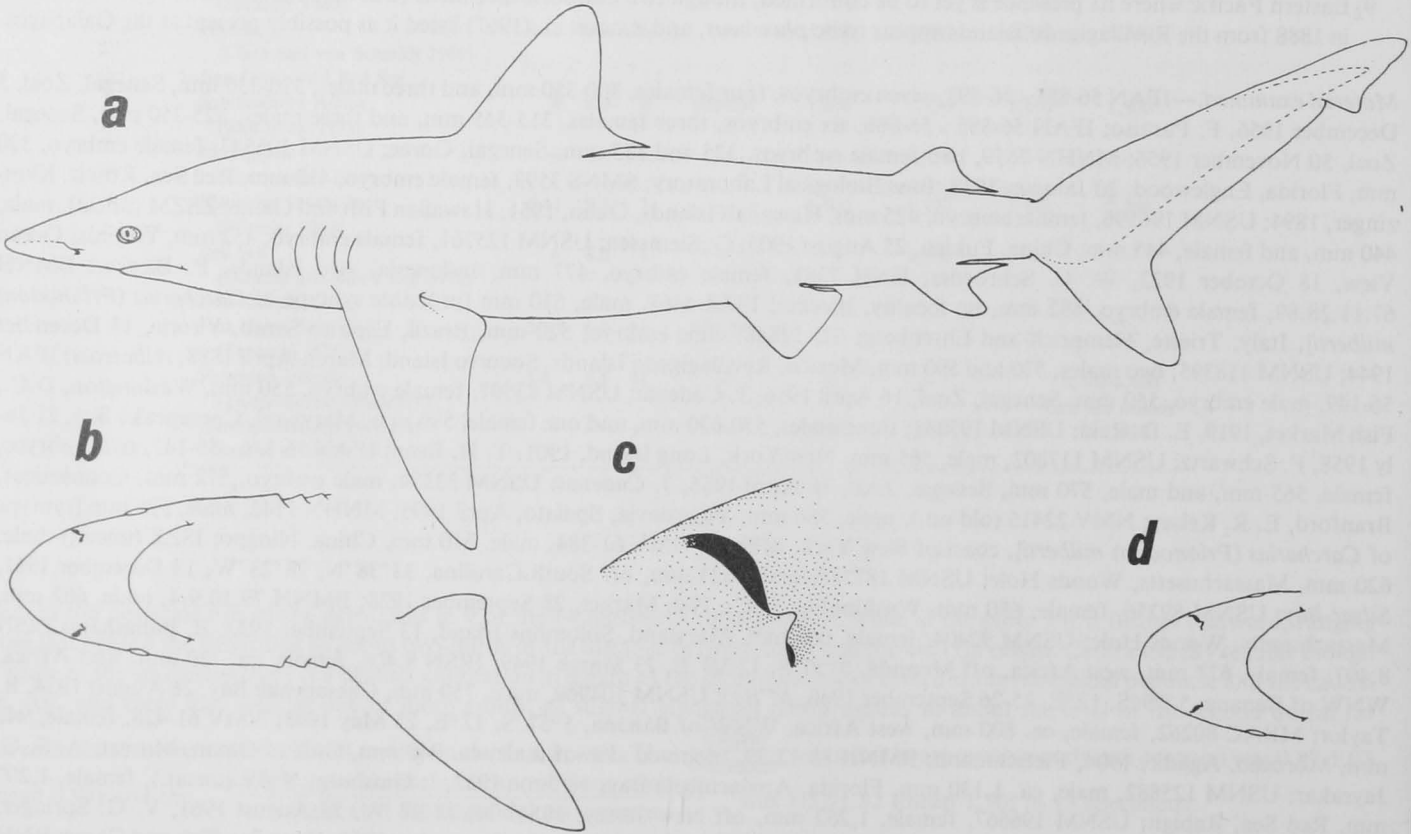


Figure 64.—*Carcharhinus altimus*, SIO 62-205, 1,530 mm TL, male from Colombia: a, left side; b, underside of head; c, enlarged left nostril; d, underside of snout of USNM 197388, 1,900 mm TL, male from eastern Pacific, Revillagigedo Islands.

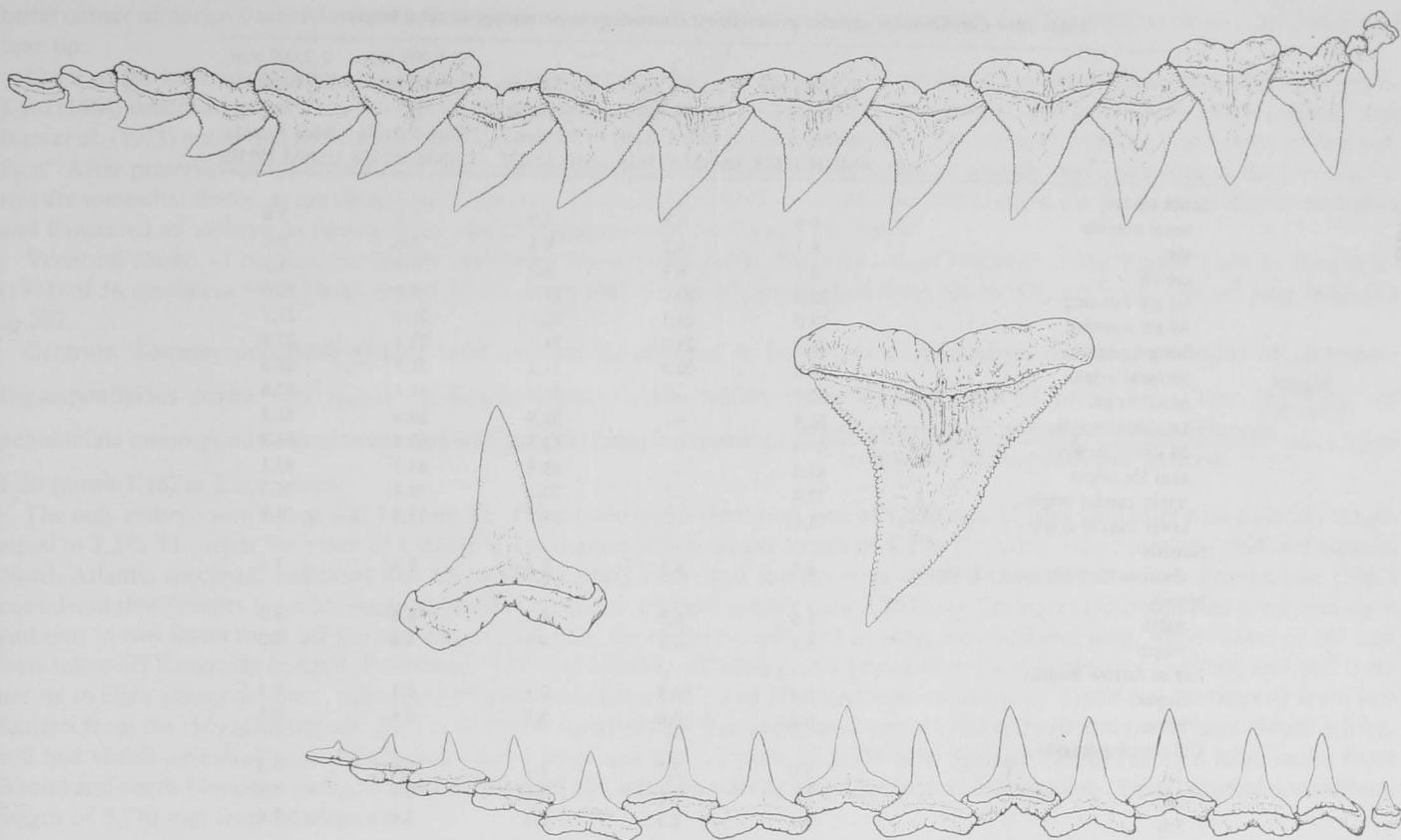


Figure 65.—*Carcharhinus altimus*, USNM 112589, 2,667 mm TL, male from Bahamas: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

Nomenclatural discussion.—The holotype of *altimus*, which is partly skinned out, was the only preserved specimen, except for jaws, available for study from the type locality (Florida), or for that matter from the western Atlantic. However, the species is sufficiently distinctive, particularly in its unusually long upper teeth, that it can be identified with confidence from other oceans despite the lack of a series of specimens for comparison. The only whole specimens of *altimus* that I have seen were from the eastern Pacific. The two smaller of these show no significant differences from the holotype although there is some variation in the shape of the snout contours. The two larger specimens differ principally in having imbricate dermal denticles whereas the holotype, and the two smaller eastern Pacific specimens, have wide-spaced, nonimbricate denticles. However, a skin sample supplied by Springer from an adult male (2,230 mm TL) from the western Atlantic also has imbricate denticles.

Fourmanoir (1961), in describing *C. radamae* from Madagascar, did not designate type material and does not appear to have deposited specimens in a museum. His account and illustrations clearly fit *altimus*. This view that *altimus* occurs in the western Indian Ocean is reinforced by photographs and jaws which I have seen in the Oceanographic Research Institute, Durban, of specimens taken off Durban, Natal, and reported by D'Aubrey (1964) and Bass et al. (1973).

Recognition of *altimus* from material from the eastern Atlantic (Senegal and the Ivory Coast) is based on jaws alone, though Cadenat (1961) has listed the species and examined specimens.

Description (see also Table 70).—Large sharks, up to about 2.8 m TL. Midline of back between dorsal fins with a low but noticeably broad, round-topped dermal ridge. Upper precaudal pit well developed, lower pit weaker.

Dermal denticles wide-spaced in specimens up to about 1,500 mm long, but contiguous to overlapping in larger specimens; denticles small, ovoid, wider than long, with three prominent longitudinal ridges and corresponding posterior marginal teeth in embryos and half-grown specimens, and five in larger specimens.

Snout long, bluntly rounded in contour in the holotype but more pointed in eastern Pacific specimens. Anterior margin of eye above front of mouth. Nostrils oblique, with broadly ovate apertures, the anterior margin of each with a prominent, narrow, pointed lobe.

Dental formula $\frac{15 \text{ or } 16-1 \text{ or } 2-15 \text{ or } 16}{14 \text{ or } 15-1-14 \text{ or } 15}$ in 16 specimens counted (10 from Senegal, 4 from the eastern Pacific, and 2 from the Bahamas and Florida); Bass et al. (1973) gave $\frac{15-1 \text{ or } 2-15}{14-1-14}$ as the usual tooth count in 28 jaws from the Natal coast of South Africa;

in some of the larger specimens the most lateral tooth on each side of the upper jaw is noticeably smaller than the penultimate tooth and could easily be overlooked in counts. Upper teeth broadly triangular, long, oblique except for first two series at each side of symphysis, their lateral margins concave, their medial margins straight to convex, both margins serrated, the serrations of moderate size; one or two small symphyseal teeth. Lower teeth narrow, erect, uniformly and finely serrated; one small symphyseal tooth.

Table 70.—*Carcharhinus altimus*, proportional dimensions in percentage of total length.

	♀ 745 mm Lower California AMNH 15678	♂ 1,321 mm Florida Keys Cosgrove Reef USNM 133828	♂ 1,530 mm Colombia Tumaco SIO 62-205	♂ 1,900 mm Revillagigedo Is. Roca Partida USNM 197388	♀ 2,007 mm Revillagigedo Is. Roca Partida USNM 197388
Snout tip to					
outer nostrils	4.4	3.8	4.0	3.5	3.8
eye	8.7	8.3	8.1	7.6	8.0
mouth	8.7	8.3	8.2	7.7	8.1
1st gill opening	20.9	20.0	19.3	18.7	19.0
3d gill opening	24.0	22.5	22.1	21.1	21.7
5th gill opening	26.8	25.0	24.2	23.1	23.8
pectoral origin	25.6	24.4	23.2	21.7	22.2
pelvic origin	52.7	—	51.4	51.6	52.6
1st dorsal origin	31.8	—	31.9	29.6	31.3
2d dorsal origin	65.4	—	63.5	63.4	63.9
anal fin origin	66.0	—	63.8	64.1	65.1
upper caudal origin	77.4	—	74.1	74.3	75.1
lower caudal origin	75.8	—	73.7	73.5	74.8
Nostrils					
distance between inner corners	6.2	6.2	5.8	5.3	5.6
Mouth					
width	7.9	8.5	8.1	8.6	8.5
length	5.1	4.8	4.6	4.4	4.2
Labial furrow lengths					
upper	0.8	0.5	0.3	0.5	0.5
lower	0.6	0.6	0.5	0.6	0.5
Gill opening lengths					
1st	3.0	2.7	3.3	3.4	3.3
3d	3.2	3.1	3.6	3.7	3.9
5th	2.3	2.3	2.3	2.4	2.6
Eye					
horizontal diameter	2.3	1.9	1.6	1.5	1.4
1st dorsal fin					
length of base	11.9	10.1	9.8	11.6	11.0
length posterior margin	4.6	5.0	5.0	4.8	4.5
height	8.3	11.9	10.5	10.2	9.9
2d dorsal fin					
length of base	4.3	4.6	3.8	4.2	4.3
length posterior margin	4.0	3.8	3.9	4.0	3.6
height	2.8	3.4	3.2	2.9	3.2
Anal fin					
length of base	4.0	3.8	4.2	3.9	4.3
length posterior margin	3.6	4.0	3.8	3.7	3.5
height	3.2	3.5	4.1	3.5	3.7
Pectoral fin					
length of base	6.2	6.5	6.9	6.7	7.1
length anterior margin	19.6	21.1	21.3	22.4	21.4
length distal margin	11.8	17.5	17.9	18.9	18.4
greatest width	10.1	11.2	11.3	11.1	11.1
Pelvic fin					
length of base	4.8	5.6	5.3	5.5	5.8
length anterior margin	6.2	6.9	6.3	6.6	7.0
length distal margin	5.0	6.3	6.4	6.1	6.4
length of claspers	—	—	3.3	8.7	—
Caudal fin					
length of upper lobe	23.3	26.9	26.5	26.7	26.2
length of lower lobe	12.1	12.5	12.6	13.7	13.2
Trunk at pectoral origin					
width	12.1	—	12.5	11.9	13.1
height	11.0	—	11.3	12.0	12.6
Dental formula	$\frac{15-1-16}{15-1-15}$	$\frac{15-2-15}{14-1-14}$	$\frac{15-2-15}{14-1-14}$	$\frac{1-15-2-15-1}{15-1-15}$	$\frac{1-15-2-15-1}{15-1-15}$
Vertebrae					
precaudal	108		110		
caudal	94		96		
total	202		206		

¹Holotype of *Eulamia altima*, a partly skinned out specimen, hence some dimensions are of doubtful accuracy.

First dorsal fin fairly high, its apex rather broad but bluntly pointed; origin of first dorsal about over axil of pectoral or slightly behind axil to as far back as almost halfway along posterior (inner) margin of pectoral. Second dorsal fin rather large and high, almost equal to anal fin; length of second dorsal rear tip 1.1-1.4 times its height; origin of second dorsal noticeably in advance of anal fin origin. Pectoral fin long, fairly broad, but pointed distally; origin of pectoral fin below or slightly in advance of fourth gill opening;

outer corner of pectoral when latter is adpressed to trunk so that anterior margin is horizontal reaches almost as far back as first dorsal rear tip.

Color of the holotype in life was said to be "... light gray above, whitish below, lower sides of pectoral tips darker" (Springer 1950). Kato (1964) described eastern Pacific specimens as having "Dorsal surface a distinct bronze-gray, undersides dirty grayish-white;" and Bass et al. (1973) noted that in South African material "The back is grey, sometimes with a coppery tint, fading into a paler ventral surface." After preservation the dorsum and sides are dark gray, the undersurface pale gray to whitish; the undersides of the pectoral fin tips are somewhat dusky, as are the apices of the second dorsal and anal fins and the tips of the caudal fin. Fourmanoir (1961) described and illustrated an embryo as having black tips or margins on all fins except the pelvic.

Vertebral counts of two eastern Pacific specimens are as in Table 70. The only counts reported in the literature are by Bass et al. (1973) of 16 specimens from Natal, South Africa; precaudal counts of these ranged from 101 to 107, while total counts were from 194 to 202.

Centrum diameter noticeably greater than centrum length even in longest monospondylous centra at posterior of abdomen. Diplospondylous centra very regular in length. Diplospondyly begins above anterior third of pelvic base. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.67 to 0.69 (mean 0.68) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.15 to 1.20 (mean 1.18) in 2 specimens.

The only embryo seen by me was 745 mm TL. Of the two males examined, one of 1,530 mm TL was immature with a clasper length equal to 3.3% TL, while the other of 1,900 mm was mature with a clasper length of 8.7% TL. Data from Springer (1960) for western North Atlantic specimens indicated that his smallest mature males and females were about 2,160 and 2,260 mm. Fourmanoir (1961) considered that females from Madagascar became mature at a length greater than 2,350 mm. Springer (1950) reported seven and eight embryos in two litters from off the east coast of Florida; the embryos, collected in May, were 610 mm long, while others of 585 mm were taken off Venezuela in April. Fourmanoir (1961) noted that off Madagascar young are born in September-October, and that there are six to eight young per litter, measuring 650-700 mm. Litters of 3 and 11 young were recorded by Tester (see footnote 4) from two females from the Hawaiian Islands. Bass et al. (1973) reported that free-living specimens of 780 and 910 mm from Natal, South Africa, still had visible umbilical scars. The largest adult I have seen was a female of 2,007 mm. Springer (1950) reported adult males from Bimini and south Florida growing to about 2,670 mm, and adult females to about 2,820 mm. Fourmanoir (1961) reported a maximum length of 2,770 mm from Madagascar.

Distribution (see also Material examined).—Although whole specimens of *altimus* are rare in museum collections, jaws are better represented. The distinctiveness of the teeth makes identification possible from jaws alone. On this basis identifications made by me on jaws as well as on whole specimens, or from the literature by Springer (1950), Cadenat (1961), Fourmanoir (1961, as *C. radamae*), D'Aubrey (1964), Kato (1964), Kato and Carvallo (1967), Kato et al. (1967), Tester (see footnote 4), Guitart Manday (1968), and Bass et al. (1973) gave *altimus* a distribution as follows: western Atlantic from off Florida (Cape Canaveral to Tortugas), the Bahamas (Bimini), Cuba, Nicaragua, Costa Rica, and Venezuela (Gulf of Paria); eastern Atlantic off Senegal and the Ivory Coast; western Indian Ocean off Natal, South Africa, and northwards off Delagoa Bay and off the west coast of Madagascar; eastern Pacific from near the Gulf of California, the Revillagigedo Islands, Colombia (Tumaco), and Ecuador; and central Pacific at the Hawaiian Islands. Springer (1950) noted that most specimens in the western Atlantic were taken in depths of 50-200 fathoms (91-366 m), which agrees with Fourmanoir's (1961) report of captures off Madagascar in 140-160 m, Bass et al.'s (1973) statement that most Natal specimens were from 250 to 430 m, and Tester's (see footnote 4) survey of Hawaiian sharks where six of nine *altimus* taken were from 80 to 196 fathoms (146-358 m) and the other three were from 15 to 25 fathoms (27-46 m). However, Cadenat²³ stated that most of the Senegal and Ivory Coast specimens he has seen were taken in 10-20 m.

Material examined.—AMNH 15678, female embryo, 745 mm, Lower California; USNM 133828, female, 1,321 mm (partly skinned out) (holotype of *Eulamia altima*), Florida Keys, Cosgrove Reef, 2 April 1947; SIO 62-205, male, 1,530 mm, Colombia, off Ensenada Tumaco, 15 March 1962; USNM 197388, mature male, 1,900 mm, and female, 2,007 mm, Mexico, Revillagigedo Islands, Roca Partida, 4 August 1962, S. Kato; USNM 112589, jaws of male, 2,667 mm, Bahamas, Bimini, 3 June 1948, S. Springer and H. R. Bullis; ORID, jaws and photographs of 20 specimens taken off Durban, Natal; IFAN, numerous jaws from Senegal (M'Bour and Joal).

Carcharhinus perezii (Poey, 1876) Figures 66, 67, 68

Platypodon Perezii Poey, 1876:194-196, pl. 14, figs. 2, 3. Six specimens mentioned, being three females of 1,300, 977, and 860 mm and two males of 800 and 780 mm, plus the head of a female of 2 m; Cuba.

Eulamia springeri Bigelow and Schroeder, 1944:30-33, pls. 9, 10. Holotype, female, 805 mm, Cozumel, Yucatan; another specimen, female, ca. 1,390 mm (head and skin), tentatively referred to *springeri* was from Englewood, Fla.

Diagnosis.—Large sharks, up to 2.95 m long, with a low interdorsal ridge; tips of paired fins, anal fin, and lower lobe of caudal dusky; snout moderately short and bluntly rounded; internarial width 1.0-1.1 in preoral length; origin of first dorsal fin over or slightly

²³J. Cadenat, Institut Français d'Afrique Noire, B.P. 206, Dakar Sénégal, pers. commun. May 1963.

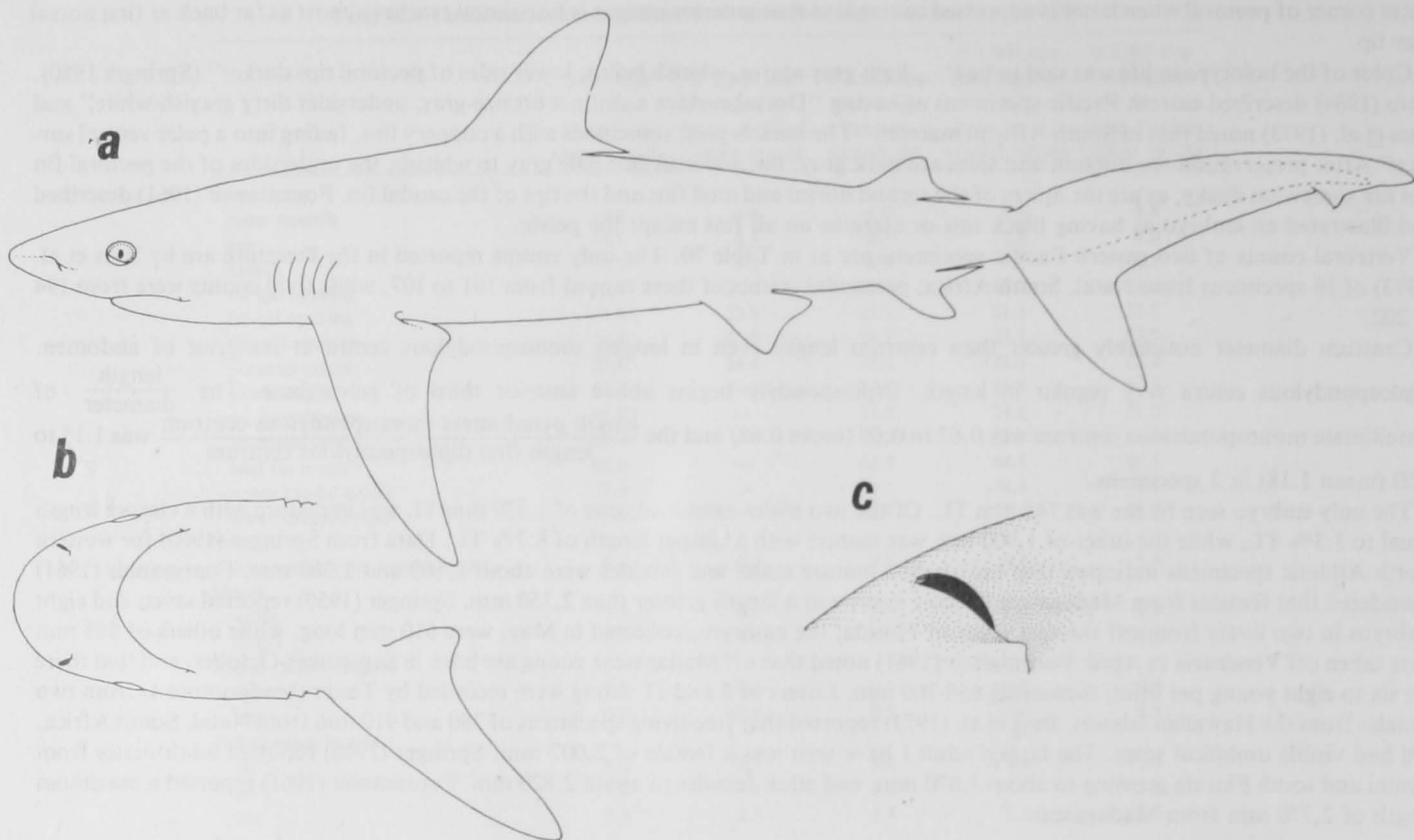


Figure 66.—*Carcharhinus perezii*, USNM 197361, 1,023 mm TL, female from Jamaica: a, left side; b, underside of head; c, enlarged left nostril.

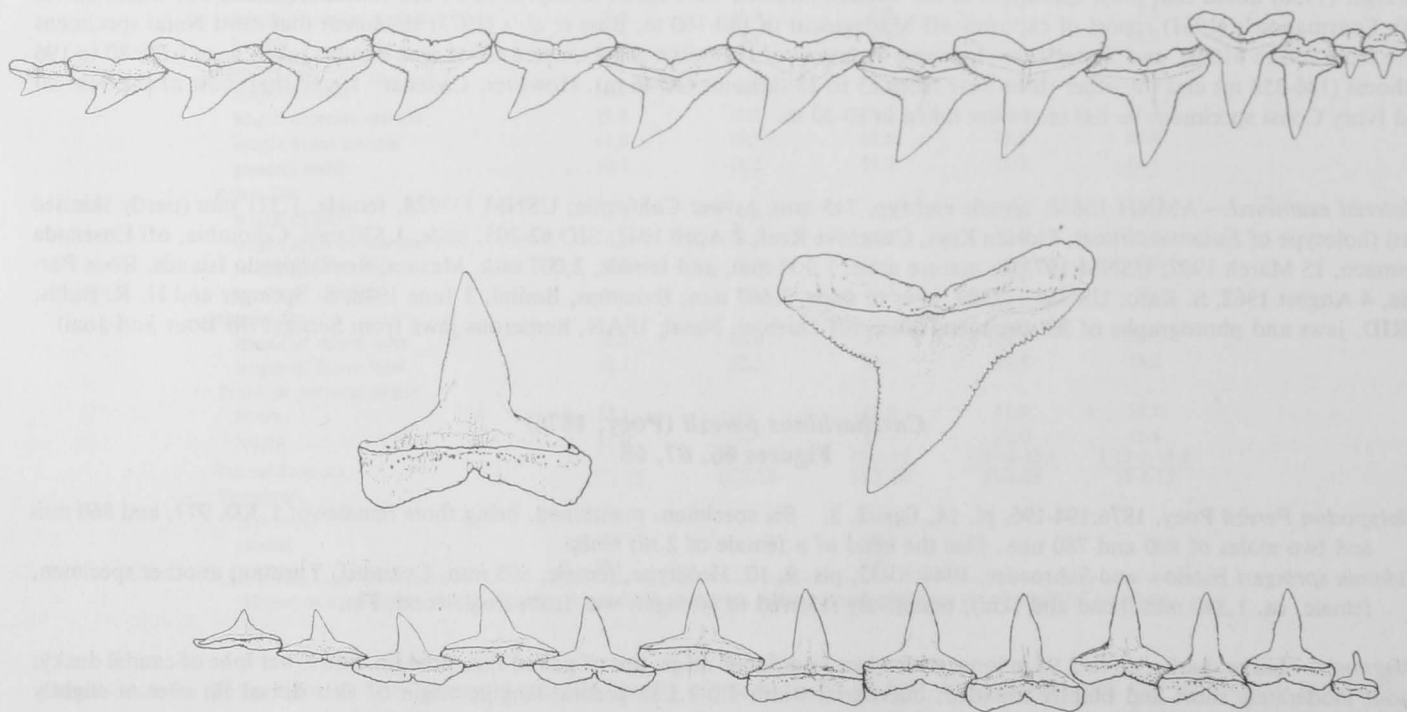


Figure 67.—*Carcharhinus perezii*, UMML 9072, from the Bahamas: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

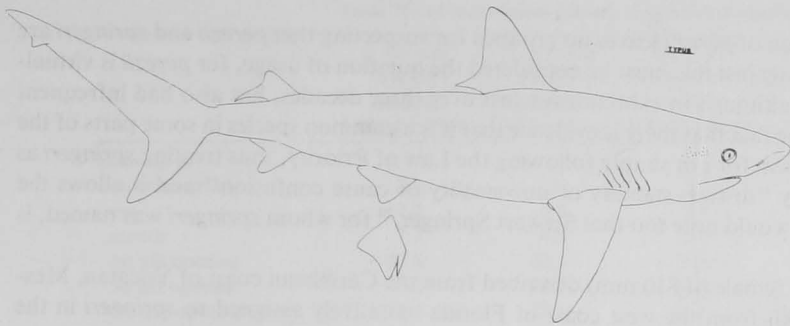


Figure 68.—Reproduction of a tracing from an unpublished drawing labelled “*Platypodon perezii*, Poey TYPUS. 29 June, 1872” from page 1533 of Atlas No. XVIII of Poey’s original manuscript of *Ictiologia Cubana*. The shark figured was said to be 1,290 mm long.

anterior to inner pectoral corner; apex of first dorsal acute to sharply rounded; origin of second dorsal about over or slightly in front of anal fin origin; height of second dorsal 2.9-3.3% TL and 1.1-1.5 in length of its rear tip; dental formula usually $\frac{13-1-13}{12-1-12}$ but may be $\frac{12 \text{ or } 13-1 \text{ or } 2-12 \text{ or } 13}{11 \text{ or } 12-1-11 \text{ or } 12}$; upper teeth moderately narrow, oblique, strongly notched laterally, concave to weakly notched medially, with slightly coarser serrations basally; lower teeth erect, serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 103-108; caudal centra 102-107; total centra 208-213; diplospondyly begins from pelvic origin to halfway along pelvic base; diplospondylous centra regular in length; penultimate monospondylous centrum 1.3-1.4 times wider than long.

This Caribbean species is remarkably similar to *galapagensis*, not only in external form but also in vertebral numbers. To a lesser extent it resembles *obscurus*, *plumbeus*, and *altimus* with which it shares, along with *galapagensis*, the common features of an interdorsal ridge, no conspicuous color pattern other than dusky fin tips, and a first dorsal fin origin which is over or anterior to the pectoral inner corner. However, *perezii* differs from all of these in the shape of its upper teeth (narrow, and strongly notched laterally rather than broad and concave laterally) and, in most cases, in its lesser number of teeth (usually $\frac{13-1-13}{12-1-12}$ whereas the other species mostly have 14 or even 15 upper teeth and from 13 to 15 lower teeth on each side).

Nomenclatural discussion.—Poey’s (1876:194) description of *perezii* from Cuba is rather general and is accompanied only by illustrations of one upper and one lower tooth. Nevertheless the description and illustrations are, in the light of present knowledge, adequate to establish the identity of the species. In particular, Poey’s account shows that *perezii* was a species of large size (the teeth he illustrated were from a female of 2 m and he mentioned a juvenile of 780 mm that still had an umbilical scar) with a short bluntly rounded snout, an acute first dorsal fin originating above the inner (posterior) corner of the pectoral fin, a second dorsal fin above or only slightly forward of the anal fin, a dental formula with a low number of teeth ($\frac{13-1-13}{12-1-12}$), teeth serrated in both jaws and the upper teeth rather narrow and oblique. Poey compared his *perezii* only with his *Eulamia obtusa* (= *leucas*) and noted differences between these two species, but if comparison is extended to the other large species of *Carcharhinus* known from the western Atlantic the characters given above exclude all of them except *springeri* (Bigelow and Schroeder 1944). This identification of *perezii* as a synonym of *springeri* is confirmed by other unpublished Poey data which has come to my attention and is considered below.

Poey’s (1876) account of *perezii* has received scant attention in the literature. Jordan and Evermann (1896) recognized *perezii* as a valid species, but Garman (1913) relegated it, without comment, to the synonymy of *remotus* (perhaps on the shape of the teeth). Bigelow and Schroeder (1944) did not mention it when they described *springeri*, but later (1948) treated it as a junior synonym of *limbatus* on the grounds of similarity in color (pectorals described as having black tips and the sides of the body with a dark band) and teeth. They also noted that “A photograph of Poey’s unpublished drawing of an adult female shows nothing to separate it from *limbatus*.”

I was unable to locate the photograph mentioned by Bigelow and Schroeder (1948) but through the courtesy of David Pérez Pérez, Escuela de Ciencias Biológicas, Universidad de la Habana, I was provided with data from Poey’s original manuscripts of his *Ictiologia Cubana*. The data include a tracing of a full-sized drawing of a shark from page 1533 of Atlas No. XVIII, which is labelled “*Platypodon perezii*, Poey TYPUS. 29 June, 1872” and has the added comment that the specimen was 1,290 mm long and the drawing 1,300 mm. A copy of this tracing is given here (Fig. 68). The shark in the drawing is one of the six which Poey (1876) mentioned in his description of *perezii*. The only disquieting feature is that Poey listed the 1,300 mm shark as a female, whereas the one in the tracing is presumably a male to judge by the separate drawing of a pelvic fin with clasper below the lateral view of the whole shark. Regardless of this discrepancy the tracing clearly fits *springeri*. Additional data sent by Pérez Pérez are translations of notes which accompanied drawings (on pages 1535-1538 of the Atlas) of four of the other type specimens. Most of the notes refer to color, and particularly to darker tips on the pectoral, pelvic, and lower lobe of the caudal fin, but one mentions lobules on the nostrils (referring to the low, pointed lobe on the anterior margin of each nasal flap) and another that there is a raphe behind the first dorsal fin. The last-mentioned item is of special value in that it obviously refers to the middorsal ridge; had Poey appreciated its importance and included it in his published description it would have led to a better understanding of his *perezii* (a middorsal ridge is present in *springeri* but not in *limbatus*). Finally, in volume III of *Ictiologia Cubana*, Poey gave the dental formula of *perezii* as $\frac{13-1-13}{13-1-13}$, thus slightly extending the count of $\frac{13-1-13}{12-1-13}$ used in his published description of *perezii* (in comparison *springeri* was described as having $\frac{12-1-13}{12-1-13}$).

The above information coupled with the original description of *perezii* leaves no grounds for suspecting that *perezii* and *springeri* are different species. The name *perezii* has obvious priority, but against this must be considered the question of usage, for *perezii* is virtually an unused name. On the other hand the name *springeri*, although in existence for just over three decades, has also had infrequent usage; *springeri* is by no means a well-known shark despite the fact that there is evidence that it is a common species in some parts of the Caribbean. Accordingly, I believe that there is no strong reason for not simply following the Law of Priority, thus treating *springeri* as a junior synonym of *perezii*; such action should not unduly "disturb stability or universality or cause confusion" and it allows the retention of a name which in retrospect was well founded. I would note too that Stewart Springer,²⁴ for whom *springeri* was named, is in agreement with this decision.

I have examined the holotype of *springeri* (USNM 37141, female of 810 mm) described from the Caribbean coast of Yucatan, Mexico, but was unable to find a second specimen (MCZ 35900) from the west coast of Florida tentatively assigned to *springeri* in the original description by Bigelow and Schroeder (1944:30).

Description (see also Table 71).—Large sharks, growing to about 3.0 m TL. Midline of back between dorsal fins with a low dermal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles close-packed, overlapping, subcircular in outline, usually slightly wider than long, each with three to five longitudinal ridges and corresponding posterior marginal teeth in small specimens, but with seven ridges and teeth in subadults and adults.

Snout moderately short, bluntly rounded in contour. Anterior margin of eye above or slightly forward of mouth. Nostrils strongly oblique, slitlike, the anterior margin of each with a low, pointed lobe.

Dental formula $\frac{13-1-13}{12-1-12}$ in five of nine specimens counted; $\frac{13-2-13}{12-1-12}$ in one; and falling within the range $\frac{12 \text{ or } 13-1 \text{ or } 2-12 \text{ or } 13}{11 \text{ or } 12-1-11 \text{ or } 12}$ in the remaining three. Upper teeth narrowly triangular, oblique except for first one or two series on each side of symphysis, their lateral margins strongly notched, their medial margins concave or even weakly notched (though distally the medial margins are convex), both margins finely serrated though the serrations are a little coarser basally; one or two small symphyseal teeth. Lower teeth narrow, erect, with both margins very finely serrated; one small symphyseal tooth.

First dorsal fin moderately high, rather narrow, its apex acute to sharply rounded; origin of first dorsal over or slightly anterior to inner (posterior) corner of pectoral fin. Second dorsal fin rather high, almost equal to anal fin; length of second dorsal rear tip 1.1-1.3 (mean 1.2) times second dorsal height in five small specimens (up to 1,082 mm long) but 1.5 times in an adult of 2,950 mm; origin of second dorsal about over or slightly anterior to anal fin origin. Pectoral fins moderately long, slender, pointed at their outer tips; origin of pectorals below and between the levels of the third and fourth gill openings; outer corner of pectoral when latter is addressed to trunk so that its anterior margin is horizontal reaches from just behind level of first dorsal axil to almost as far as first dorsal rear tip.

Color after preservation in alcohol is dusky gray or grayish brown above, pale or white below; undersides of paired fins dusky (but not black) at their tips and trailing margins; tips of anal fin and of lower lobe of caudal fin similarly dusky.

Vertebral counts of six specimens are given in Table 71 and of another two specimens in Table 72.

Centrum diameter noticeably greater than centrum length even in longest monospondylous centra at posterior of abdomen. Diplospondylous centrum length regular. Diplospondyly begins above anterior to middle of pelvic base. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.69-0.74 (mean 0.71) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.16-1.26 (mean 1.21) in 4 specimens.

The smallest, free-living specimen I have seen was 726 mm TL, and the only embryos were 265 and 290 mm. One of the syntypes of *perezii*, a male of 780 mm, was described by Poey (1876) as still showing an umbilical scar, and the same applies to the 810 mm female holotype of *springeri* (Bigelow and Schroeder 1944). I have seen no males other than the two embryos, and have found no data on males in the literature. The female from which the embryos were obtained was about 2,000 mm long. Cervigon (1966) reported that a female of 2,240 mm from Venezuela contained four embryos. The largest specimen known to me is the female of 2,950 mm listed here from the Bahamas.

Distribution (see also Material examined).—*Carcharhinus perezii* was first described from Cuba, and its only synonym, *springeri*, was based on a holotype from off the east coast of Yucatan, Mexico (plus another specimen tentatively referred to *springeri* from the west coast of Florida). The species is poorly represented in museum collections, and the few specimens that I have seen extend its distribution only to more of the Caribbean. Localities include the Bahamas, off Jamaica, the Virgin Islands, and Barbados. Cervigon (1966, as *springeri*) reported three specimens from Los Hermanos Islands, Venezuela. However, despite these few records *perezii* cannot be uncommon, for Springer (1960, as *springeri*), in describing the catches from experimental shark fishing off the western edge of the Bahamas Bank, noted that of 447 sharks caught, 197 were *perezii* which was, therefore, easily the most abundant species. Springer also reported that test fishing off the mouth of the Mississippi River produced one specimen of *springeri*, and he further observed that *perezii* occurs off Salerno on the east coast of Florida. Randall (1963b, as *springeri*) similarly noted that *perezii* is "... not uncommon in the Caribbean. It has been caught more often than any other shark, except the nurse shark, by the author and associates in connection with studies of reef fishes in Puerto Rico and the Virgin Islands." Clark (1975, as *springeri*) reported *perezii*, including colored plates of the species in life, from underwater caverns off Isla Mujeres, Yucatan, Mexico.

²⁴Stewart Springer, Fishery Biologist, Bureau of Commercial Fisheries, Systematic Laboratory, U.S. National Museum, Washington, DC 20560, pers. commun. June 1969.

Table 71.—*Carcharhinus perezii*, proportional dimensions in percentage of total length.

	♀ 726 mm SW of Jamaica USNM 197361	¹ ♀ 810 mm Mexico Cozumel USNM 37141	♀ 915 m Virgin Is. Tobago USNM 196005	♀ 1,023 mm SW of Jamaica USNM 197361	♀ 1,082 mm Bahamas Cat Cay UMML (uncat.)	² ♀ 1,900 mm Venezuela Los Herma- nos Is.	♀ 2,950 mm Bahamas Grand Bahama
Snout tip to							
outer nostrils	3.1	3.0	3.2	3.0	2.8	2.9	2.6
eye	7.2	6.6	6.8	6.9	6.7	—	6.1
mouth	7.7	6.4	6.9	7.1	6.9	6.5	6.1
1st gill opening	20.0	20.2	19.0	19.3	18.1	—	18.6
3d gill opening	22.0	22.2	21.6	21.4	19.7	—	21.3
5th gill opening	23.8	23.5	23.4	23.1	21.1	—	23.2
pectoral origin	22.3	22.0	22.0	21.7	20.3	—	22.2
pelvic origin	48.9	48.2	49.7	49.3	48.2	—	53.6
1st dorsal origin	31.4	30.8	32.2	31.5	30.5	33.6	33.2
2d dorsal origin	60.6	60.0	60.6	60.6	60.2	66.5	65.7
anal fin origin	60.9	59.7	60.6	61.8	59.9	—	66.1
upper caudal origin	71.7	71.7	71.9	72.0	71.1	—	75.8
lower caudal origin	71.2	70.7	71.1	71.2	70.2	—	75.5
Nostrils							
distance between inner corners	7.2	6.5	6.8	6.8	6.9	—	5.9
Mouth							
width	9.4	8.5	8.7	9.7	9.9	9.6	8.9
length	5.1	4.9	5.5	5.1	5.7	4.8	4.7
Labial furrow lengths							
upper	0.3	0.4	0.5	0.3	0.5	—	0.3
lower	0.6	0.6	0.7	0.4	0.6	—	0.6
Gill opening lengths							
1st	2.8	2.3	2.9	2.4	2.6	3.2	2.7
3d	3.2	2.8	3.2	2.9	3.4	4.0	3.3
5th	2.6	2.0	2.2	2.3	2.2	2.3	2.9
Eye							
horizontal diameter	2.5	2.0	2.2	2.0	2.1	1.8	1.2
1st dorsal fin							
length of base	10.2	9.6	9.6	8.7	9.7	10.1	11.1
length posterior margin	3.2	3.0	3.3	3.4	3.4	—	3.3
height	11.3	10.3	11.2	10.3	11.2	10.3	10.7
2d dorsal fin							
length of base	4.1	4.0	4.4	4.1	3.9	3.9	3.6
length posterior margin	3.8	3.5	3.5	4.1	3.9	—	4.2
height	3.3	3.1	2.9	3.0	3.2	3.1	2.9
Anal fin							
length of base	4.5	4.9	4.5	4.3	4.2	4.1	4.2
length posterior margin	3.4	3.1	3.4	3.7	3.6	—	3.5
height	3.6	3.5	3.6	3.4	3.7	3.7	3.7
Pectoral fin							
length of base	6.0	6.0	5.5	6.1	5.6	—	7.1
length anterior margin	20.0	19.5	20.0	20.3	20.3	20.8	21.7
length distal margin	16.9	15.4	16.5	16.5	16.8	19.4	20.2
greatest width	—	8.8	9.0	—	9.6	—	—
Pelvic fin							
length of base	5.2	4.7	4.8	5.3	4.9	—	5.5
length anterior margin	6.2	5.5	5.9	6.2	6.1	—	6.1
length distal margin	5.8	5.2	5.8	5.7	5.7	—	6.9
length of claspers	—	—	—	—	—	—	—
Caudal fin							
length of upper lobe	29.5	29.0	28.9	28.3	29.2	30.6	27.0
length of lower lobe	16.9	13.9	13.5	13.6	13.9	14.3	13.9
Trunk at pectoral origin							
width	13.5	11.7	11.8	13.4	12.7	—	—
height	11.8	11.5	12.3	11.4	10.3	—	—
Dental formula	$\frac{12-1-12}{12-1-12}$	$\frac{12-1-13}{12-1-12}$	$\frac{13-1-13}{11-1-11}$	$\frac{13-1-13}{12-1-12}$	—	$\frac{13-?-13}{?-?-?}$	—
Vertebrae							
precaudal	105	106	105	106	108	—	104
caudal	104	107	103	103	102	—	106
total	209	213	208	209	210	—	210

¹Holotype of *Eulamia springeri*.²Dimensions of specimen from Cervigon (1966).

Material examined.—USNM 196004, two male embryos, 265 and 290 mm (from female, ca. 2,000 mm, listed below as USNM 196003), Virgin Islands, St. John, Lesser Lameshur Bay, 1 February 1961, R. E. Schroeder; USNM 197361, two females, 726 and 1,023 mm, off Jamaica, 17°09'N, 78°57'W, 17 May 1962, Oregon; ISZZ 4477, female, ca. 740 mm, Barbados, Schomburgh; USNM 37141, female,

Table 72.—Vertebral numbers in two specimens of *Carcharhinus perezi*.

Specimens			Precaudal	Caudal	Total
USNM 19004	Virgin Is.	sibling	103	99+	202+
USNM 19004	Virgin Is.	embryos	103	99+	202+
Range (including counts from Table 71)			103-108	102-107	208-213

810 mm (holotype of *Eulamia springeri*), Mexico, Yucatan, Cozumel Island, 22 January 1885, *Albatross*; USNM 196005, female, 915 mm, Virgin Islands, Tobago, 17 February 1961, J. Randall; UMML (uncat.), female, 1,082 mm, Bahamas, Cat Cay, 3 August 1961; USNM 196003, jaws, fins, and photograph of female, ca. 2,000 mm, Virgin Islands, St. John, Lesser Lameshur Bay, 1 February 1961, R. E. Schroeder; female, 2,950 mm (discarded), Bahamas, Grand Bahama, ½ mi off West End, 26 May 1962, *Sea Hunter*.

Also six sets of jaws, five from specimens taken at Brown Cay and Orange Cay, Bahamas (UMML 9072, 9073, 9074, 9075, 9076), and one from Brewster Reef, Fla. (UMML 8612).

Carcharhinus longimanus (Poey, 1861)

Figures 69, 70, 71

Squalus (carcharias) maou Lesson, 1830:91-93, pl. 1. Two specimens, about 1,220 mm long to base of tail, Paumotu Archipelago.

Squalus longimanus Poey, 1861:338-339, pl. 19, figs. 9, 10. Male, 1,640 mm, Cuba.

Carcharias insularum Snyder, 1904:513-514, pl. 1, fig. 1. Holotype, male, 2,130 mm, Hawaiian Islands, Oahu; paratypes, two embryos from a litter of seven, from a large female taken at the Hawaiian Islands between Molokai and Oahu.

Pterolamiops magnipinnis Smith, 1958a:132-134, pl. 1, text fig. 1, C. Female, 1,350 mm, South Africa, off Port Elizabeth.

Pterolamiops Budkeri Fourmanoir, 1961:76-77. Measurements and brief description of two specimens, one of 2,590 mm (sex not stated), the other a female of 2,630 mm, from the west coast of Madagascar; no mention of type material being deposited.

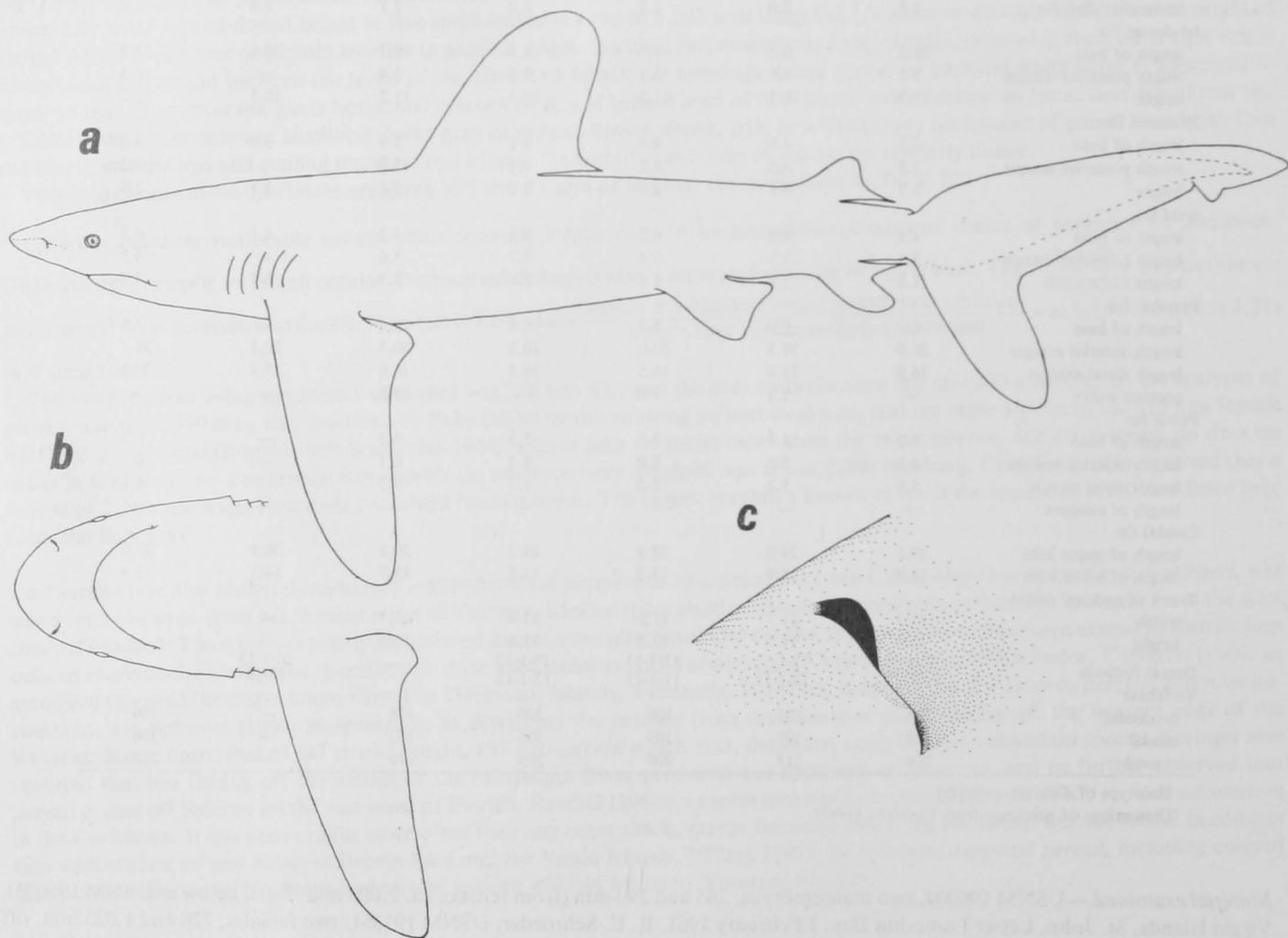


Figure 69.—*Carcharhinus longimanus*, USNM 197423, 1,670 mm TL, female from Indo-Pacific: a, left side; b, underside of head; c, enlarged left nostril.

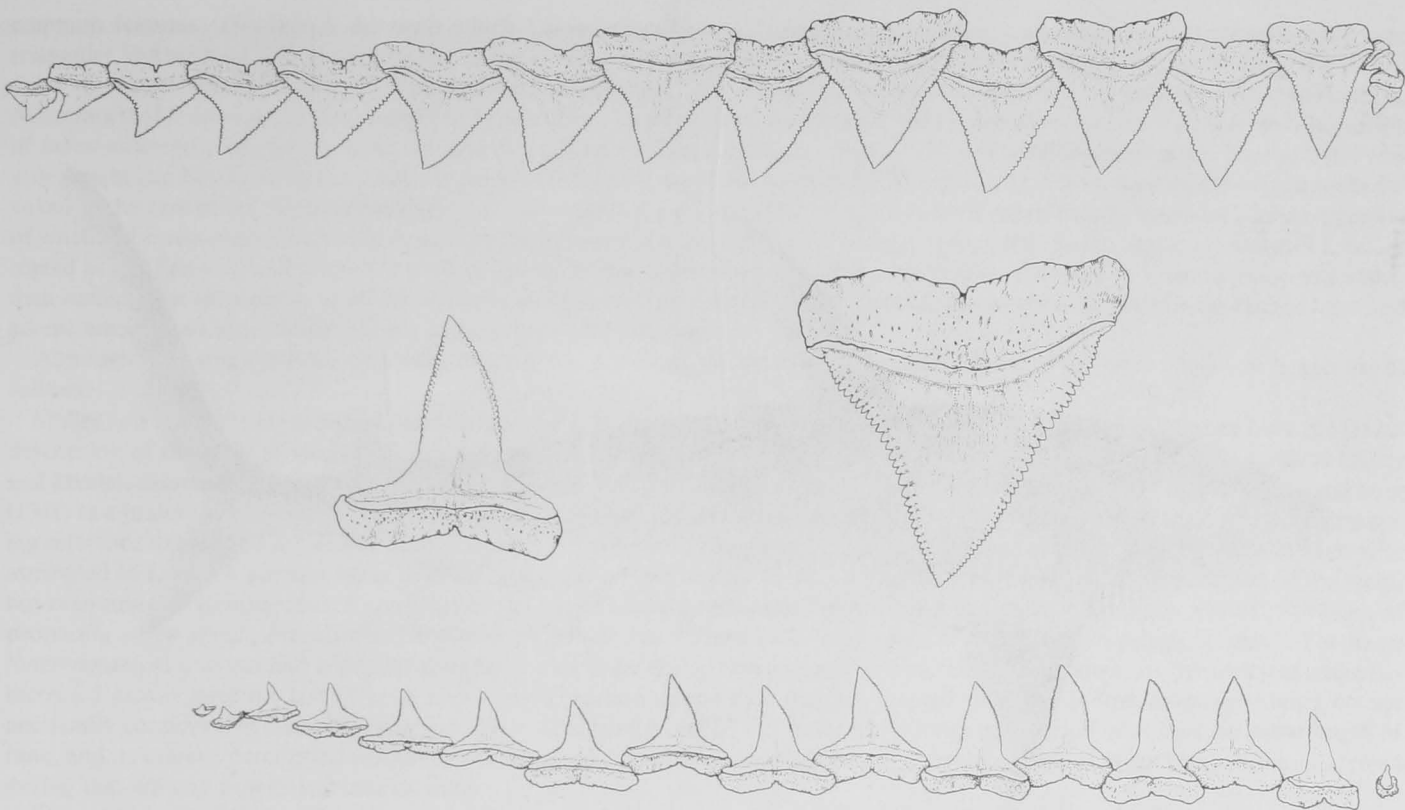


Figure 70.—*Carcharhinus longimanus*, USNM 196022, 1,969 mm TL, male from central Pacific: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

Diagnosis.—Large sharks, up to 3.00 m long, usually with a low interdorsal ridge; tips of fins, and particularly the first dorsal, pectoral, pelvic, and caudal, obviously mottled with white, but in small specimens there are black tips or blotches on most fins and notably on the pelvic, second dorsal, anal, and lower caudal; these black marks, plus black saddles at the second dorsal axil, upper caudal origin, and sometimes on the back between the dorsal fins, diminish or fade in adults; snout short and rounded; internarial width 1.0-1.2 in preoral length; origin of first dorsal fin slightly anterior to inner pectoral corner; apex of first dorsal broadly rounded due to the fin being only slightly tapered distally; origin of second dorsal in front of or over anal fin origin; height of second dorsal 2.7-3.9% TL and 1.0-1.2 in length of its rear tip; dental formula usually $\frac{14-2-14}{14-1-14}$ but may be $\frac{13 \text{ or } 14-1 \text{ or } 2-13 \text{ or } 14}{13 \text{ to } 15-1 \text{ to } 3-13 \text{ to } 15}$; upper teeth broad, erect to slightly oblique, weakly to moderately concave laterally, uniformly serrated; lower teeth erect, serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 123-131; caudal centra 106-110; total centra 228-238; diplospondyly begins from one-third to halfway along pelvic base; diplospondylous centra regular in length; penultimate monospondylous centrum 1.7-2.1 times wider than long.

The only other species with white fin tips is *albimarginatus*, but its white markings are not mottled and they extend regularly along the trailing margins of the fins. Also, the first dorsal apex of *albimarginatus* is obtusely pointed or acute. In *Carcharhinus wheeleri* only the first dorsal tip and trailing margin are white, the other fins, and especially the trailing margin of the caudal, having dusky to black markings.

Nomenclatural discussion.—This species, the white-tip, has become well known by the specific name *longimanus* Poey, 1861, which name I adopt here despite evidence that *longimanus* is a junior synonym of *maou* Lesson, 1830, as are also the later described *insularum* Snyder, 1904, *magnipinnis* Smith, 1958a, and *budkeri* Fourmanoir, 1961. Although, as discussed below, there could be divergence of opinion on the strength of this evidence, and on the claim that *longimanus* should be favored because it has achieved well-established usage, this seemingly is irrelevant in the light of Opinion 723 of the International Commission on Zoological Nomenclature (1965) in which *longimanus* Poey was placed on the Official List of Specific Names in Zoology (Name No. 2059). Such a placing appears to establish preference for *longimanus* even though the standing of *maou* versus that of *longimanus* was not discussed or considered. The reason for the latter is that the main thrust of Opinion 723 was to stabilize the generic names *Carcharhinus*, *Carcharodon*, and *Odontaspis*; in the case of *Carcharodon* a white-tip shark was involved as part of a composite species, and that component had to be excluded. The name *longimanus* was used to identify the white-tip, but without consideration of its priority relative to other white-tips (except to note that *longimanus* "is now well established") and to the effect on priority of putting *longimanus* on the Official List.

The most recent (1964) International Code of Zoological Nomenclature is peculiarly reticent about the status of names put on the Official Lists. However, Article 77(5) describes them as "accepted" names, which seems open to the interpretation given in the detailed statement (1950) by the International Commission on Zoological Nomenclature, and which I assume is still the intent of the Official List, that a "... name once stabilised in this way is to be used in preference to any other name for the species in question and the trivial

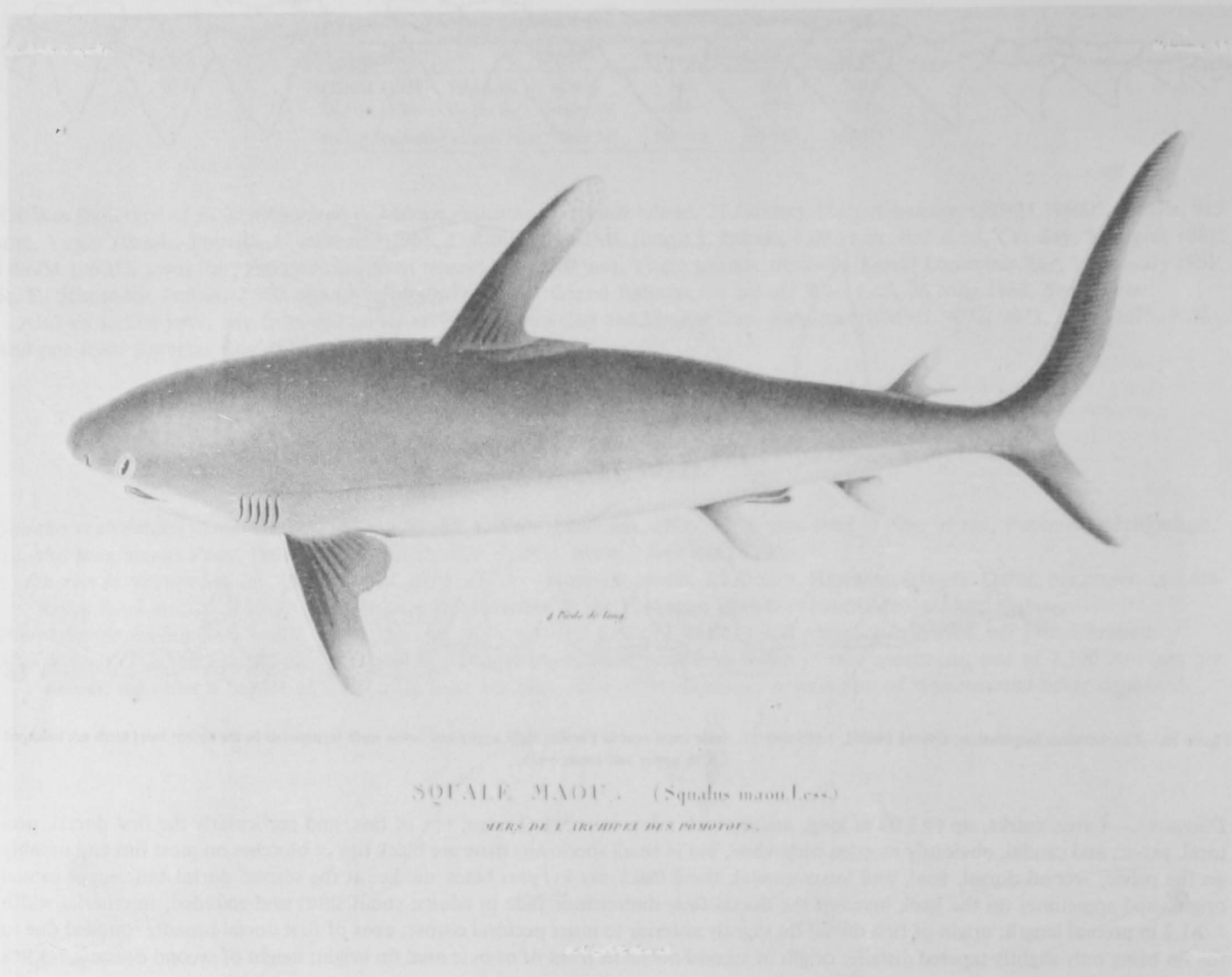


Figure 71.—Reproduction of illustration which accompanied Lesson's (1830) description of *Squalus maou*.

name in question is not to be replaced by any other trivial name, even if later it is found either (1) that the trivial name in question is not an available name or (2) that it is not the oldest available trivial name for the species in question, unless, and until, on the facts being laid before the Commission, the Commission shall so direct."

The best early description of the white-tip is that of Müller and Henle (1841:37) as *Carcharias (Prionodon) lamia*, a name which they attributed to Risso but which is not valid for the white-tip either from Risso's or previous authors' accounts because *Carcharias lamia* had first been used by Rafinesque (1810:44) as a replacement name for *Squalus carcharias* Linnaeus 1758 (= *Carcharodon carcharias*) and has since been rejected by the International Commission on Zoological Nomenclature (1965, Opinion 723, p. 33). Various accounts both prior and subsequent to that of Müller and Henle also treated the white-tip as *lamia*, but in many of them the situation was complicated by confusion with other species including *Carcharodon carcharias*, *Galeocerdo cuvieri*, and seemingly more than one species of *Carcharhinus*. The history of the nomenclatural tangle which involves the name *lamia* as one of its elements has been covered adequately by Boeseman (1960) and White et al. (1961) and need not be repeated here.

Lesson's (1830:91) account of *maou* was based on two specimens from the Paumotu Archipelago in the central Pacific, whose "longueur était de 4 pieds, sans y comprendre la queue." This precaudal length, when examined in terms of *Carcharhinus* species in general and "*longimanus*" in particular, suggests that the type specimens were about 1,650 mm TL. The type specimens were not kept, but instead, according to Lesson (1830:93), were fed to the crew of the *Coquille* who found the flesh "délicate." The description, and the accompanying illustration of *maou* which is reproduced here (Fig. 71), are of an unusual shark. Setting aside Lesson's remarks on the teeth, the description and illustration conform to *Carcharhinus* and are notable in the following features: The snout is very short and blunt; the first dorsal fin is very high; the apex of the first dorsal and the tips of the pectoral and lower lobe of the caudal are bluntly rounded; and the apices of the first and second dorsal fins and the tip of the pectoral are white but flecked or speckled with the body color. These features, which are mentioned in the description as well as being shown in the illustration, are definitive of "*longimanus*" or white-tips and do not fit any other carcharhinid. There are, however, two features which do not agree with "*longimanus*" and which were cited by Duméril (1865:379) as grounds for not combining *maou* and *lamia* (= *longimanus*) even though these two species shared

common features. The first is the teeth which Lesson described as "triangulaires et lisses," whereas those of "*longimanus*" are triangular and serrated. The second is the relative position of the second dorsal and anal fins, for in the illustration of *maou* the second dorsal is shown entirely behind the anal while in "*longimanus*" the second dorsal origin is somewhat in advance of the anal origin. Assuming that *maou* was, in fact, based on "*longimanus*," and I cannot believe that there is any alternative to this, then the illustration of *maou* as a whole was poorly executed, and must be accepted as a caricature rather than a faithful representation. On this basis very little weight can be placed on the artist's rendition of the position of the second dorsal and anal fins. The same argument cannot be invoked in the case of the statement that the teeth of *maou* were smooth. The interpretation of *maou* hinges, therefore, on the question of whether Lesson made an error in describing the nature of the teeth. If he did make an error, then *maou* can, very reasonably, be accepted as the first available name for a white-tip. If, on the other hand, Lesson's statement on the teeth of *maou* is taken as correct, then *maou* is not identifiable at all despite its other trenchant characters which delineate it as a white-tip. I favor the former view and accept *maou* as an identifiable species, synonymous with *longimanus*.

Although the name *maou* has not had extensive use, it is by no means a forgotten name. Some of the more important usages are as follows.

Müller and Henle (1841) accepted *maou* and placed it in the subgenus *Prionodon* (species with serrated teeth) despite Lesson's (1830) description of the teeth as smooth. Dumeril (1865) commented on this, and also noted its similarity to the white-tip (*lamia* of Müller and Henle). Garman (1913) treated it as a separate species. Fowler (1928) included it as a junior synonym of *commersonii*, and later (1941) as a junior synonym of *lamia*; in both these cases other white-tips were also listed as junior synonyms. Whitley (1940) made passing reference to *maou* as a "whaler shark." In view of the above usages, the failure to appreciate the true identity of *maou* cannot be attributed to Lesson's account being overlooked or inaccessible. Rather it was due in part to Lesson's faulty description of the teeth, but even more so to inadequate knowledge of the nature and characteristics of white-tips generally. As recently as 1950, Springer, in proposing a new genus, *Pterolamia*, for white-tips, noted that "*Pterolamia longimanus* is a little-known pelagic species." The name *longimanus* had thus not had a long history of well-established usage, even though it is currently well known. Its frequency of usage has increased greatly over the last 25 yr or so—a small fraction of the time that has elapsed since it was first described—but I do not necessarily consider that a strong reason for favoring it against *maou*. The latter has priority by a period of at least the same length of time, and its original description (excepting the teeth) and illustration are as good or better than those of many other species described during that era and now recognized as valid.

The status of the five nominal species of white-tips, including *maou*, has been by no means clear. Statements about the species, either in the original descriptions or subsequent accounts, suggest that some of them at least are separable on what appear to be strong differences in proportions (particularly those involving lengths or heights of fins), in fin tip shapes, and in color. These differences were lent support by the geographic separation of some of the nominal species, though *maou* and *insularum* were both described from the central Pacific, and *magnipinnis* and subsequently *budkeri* from the western Indian Ocean. No account was based, however, on an examination of an adequate series of specimens from all oceans, nor was there a description of a series covering the whole range of growth in any one species.

Springer (1960:9) gave the lengths of the pectoral fins of an embryo, a young specimen, and an adult of *longimanus* from the western North Atlantic, which showed that the young specimen, about one-third grown, had proportionately much longer fins than either the embryo or the adult. This observation, interpolated in an extensive account of another species of *Carcharhinus*, is a major clue to an understanding of the relationships of the nominal species of white-tips.

The observation suggested what appeared to be an unusual pattern of allometric growth in *longimanus*, in which the pectoral fin length would have to first progressively increase relative to total length and then subsequently decrease. This pattern can now be confirmed, and it applies to all the nominal species of white-tips. The pattern is not confined to pectoral fin growth, but also operates on the lengths of the pelvic and caudal fins and the heights of the median fins (first and second dorsals and anal). The change in the rate of growth of these fins from an increasing rate to a decreasing rate relative to increase in total length, occurs when specimens are about half adult size. Bass (1973), in his valuable and substantive account of variation and growth in three families of galeoid sharks, has demonstrated that this growth pattern is not, in fact, unusual in carcharhinid sharks, though he had insufficient juvenile specimens to confirm it for the white-tip which he recognized as *longimanus*. However, the unusual feature for the white-tips is the magnitude of the changes in fin lengths and heights.

Figures 72(a) and 72(b) illustrate this growth change phenomenon in respect to the first dorsal fin and the pectoral fin in white-tips from all oceans. The figures are based on data from several sources including the original descriptions of the nominal species, except for *insularum* where I examined the types and was unable to reconcile my measurements with those given by Snyder (1904). In consequence, for *insularum* the data used are mine. For *maou* the total length was extrapolated, as mentioned above, from Lesson's figure of 4 ft (1,219 mm) for body length excluding caudal, to 1,650 mm. The height of the first dorsal for *maou* was given by Lesson as "10 pouces a 1 pied" which, in relation to the extrapolated total length, would be from 15.4 to 18.5% TL—I have used an average of 16.9%. Because of the rather general statements given by Lesson of the proportions of *maou*, not much significance can be placed on them, and to a lesser extent this applies also to Poey's data for *longimanus*.

Figures 72(a) and 72(b) do not support the view that there are different species of white-tips separable by differences in first dorsal heights and pectoral fin lengths. Instead the figures only reflect the fact that the type specimens on which the species were based happened, for the most part, to be different in size (total length) and hence had fin-size differences reconcilable with the stage they had reached in progressing through their allometric growth pattern. Other differences said to separate the species can now also be shown to vary with growth. The most important of these are: that some fin tips, and especially the pectoral and the lower lobe of the caudal, which are bluntly rounded in young specimens become more or less angular in adults; the length of the head decreases relative to total length with growth; and there is a change in color pattern, with young specimens having some or all of the fins black tipped or with black splotches which diminish or fade with growth leaving the white-tips usually flecked with the body color in adults.

In light of the above discussion on growth change, and from an examination of all the type material that is available, I am unable to

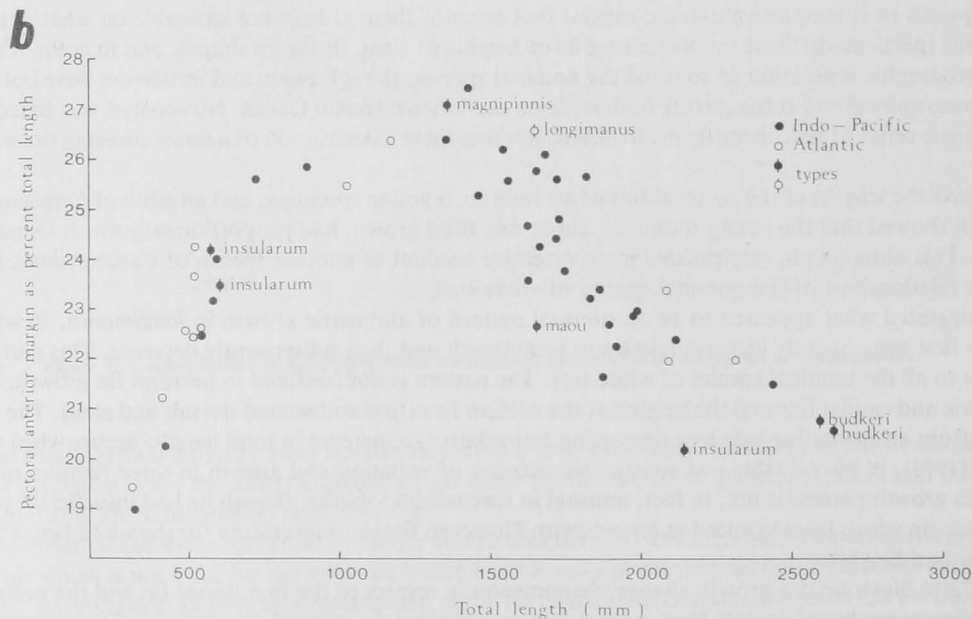
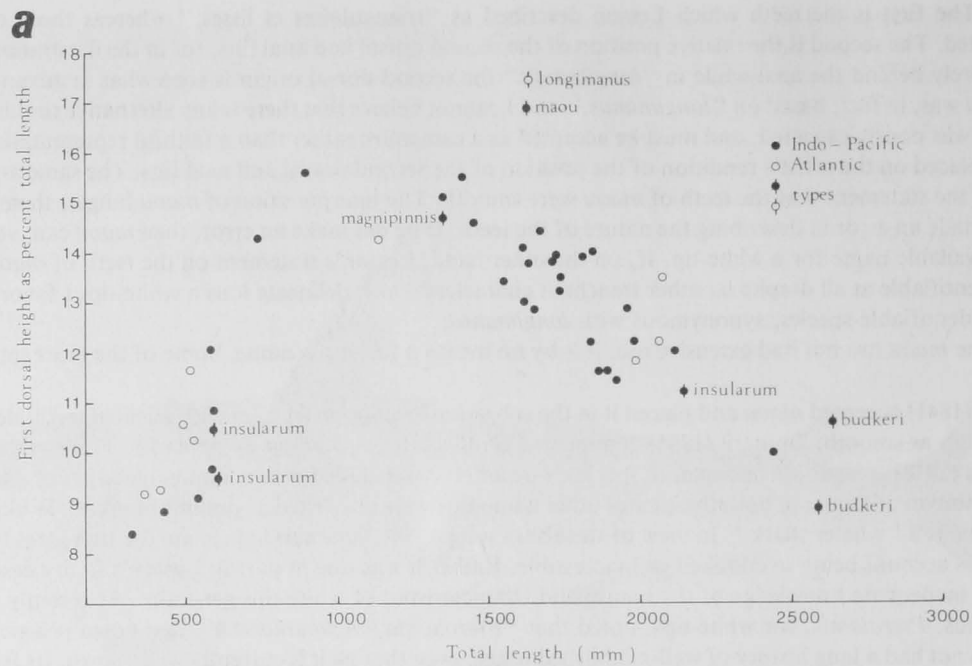


Figure 72.—Pattern of growth change in the first dorsal and pectoral fins of *Carcharhinus longimanus* based on specimens from the Atlantic and Indo-Pacific and including data from the types of the nominal species synonymized with *longimanus*: *a*, first dorsal fin height as percent of total length versus total length; *b*, pectoral fin anterior margin as percent of total length versus total length.

find any reason from my data for recognizing more than one species of white-tip. Confirmatory evidence for this view is provided by vertebral counts (see p. 157) which are remarkably high for *Carcharhinus* and show little variation.

Comments on the nominal species are given below, excluding *maou* which has already been dealt with.

Poey's (1861:338) description of *longimanus* was based on a male specimen of 1,640 mm TL from Cuba. I have no information as to whether this type is still in existence. Although Poey did not illustrate *longimanus* other than for the teeth, his description is very clearly that of a white-tip and has long been accepted as such. Poey compared his species only with *Squalus lamia* of Risso which he believed to be distinct in various features of proportions and fin shapes, and in the shape of the teeth. These differences have not been substantiated or accepted, and cannot be clarified because of the possibility that Risso's accounts involved *Carcharodon carcharias* as well as a white-tip. Recent interpretations of *longimanus* have primarily been based on the account in Bigelow and Schroeder (1948) where

measurements were given of two adults of 2,070 and 2,075 mm, and comments were made of differences in proportions and fin shapes between these adults and some late embryos.

Snyder (1904:514) described *insularum* from an adult male, 2,130 mm TL, and from seven embryos from the Hawaiian Islands. The only comment made on *insularum* was that it "... appears to be closely related to *Carcharias lamia* Rafinesque, of the Atlantic." Measurements of the adult male given in Snyder include a pectoral fin length of 390 mm or 18.3% TL—which would indicate an impossibly short-finned white-tip in terms of the total length. Measurements of the pectoral taken from Snyder's illustration suggest that this fin was 22.3% TL, while measurements which I made from the holotype (USNM 50859) give a figure of 20.2%. These and other discrepancies between Snyder's quoted measurements, the proportions shown in his illustration, and measurements which I have taken from the holotype, can only mean that he made his measurements in an unusual fashion. The consequence of them is that they have been a source of confusion to later workers and have contributed to the recognition of additional species. In Table 73 I give a set of measurements from the holotype of *insularum*, which although of doubtful accuracy in some cases because the specimen has been reduced to a skin, do show that *insularum* is not essentially different in its proportions.

Smith's (1958a:132) description of *magnipinnis* was based on a single female specimen, 1,350 mm TL, from South Africa. Smith distinguished his species from *longimanus* and *insularum* on features of pectoral fin length and first dorsal fin height relative to various head and trunk lengths, and on color pattern, but I find that from my data and from an examination of the type in the Department of Ichthyology, Rhodes University, that these features are all explainable either in terms of growth change, misinformation regarding the proportions of *insularum*, or individual variation.

Fourmanoir's (1961:76) account of *budkeri* as a new species was made from two large adults of 2,590 and 2,630 mm from off Madagascar. Apparently no type material was retained. The new species was distinguished from *longimanus* in having a lower first dorsal fin, and from *magnipinnis* in the same feature and in having a somewhat pointed tip to the lower lobe of the caudal fin. Because *budkeri* was based on specimens which were larger in size than any described as either *longimanus* or *magnipinnis*, it is not surprising in view of the information given here on growth change that Fourmanoir found differences in proportions and fin shapes which could now be predicted.

Description (see also Table 73).—Large sharks, growing to at least 3.0 m TL. Midline of back between dorsal fins with a low dermal ridge which in some specimens is not very conspicuous or occasionally may be absent (Kato et al. 1967). Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles close-packed, slightly to moderately overlapping, ovoid in outline, considerably wider than long, each with three, five, or seven longitudinal ridges and a corresponding number of short, posterior marginal teeth depending on the size of the specimen they are from.

Snout short and rounded in contour. Anterior margin of eye above front of mouth in small specimens and subadults, but slightly behind this level in adults. Nostrils strongly oblique, slitlike, the anterior margin of each almost straight except for a very short lobe.

Dental formula $\frac{14-1 \text{ or } 2-14}{14-1 \text{ to } 3-14}$ in 7 of 10 specimens counted; $\frac{14-2-14}{13 \text{ or } 14-1-13 \text{ or } 14}$ in 2; and $\frac{14-1-14}{15-1-15}$ in 1. Upper teeth broad, slightly oblique except for the first few series at each side of symphysis, their lateral margins weakly to moderately concave except on the outermost two or three teeth which are notched, their medial margins weakly sinuous, both margins coarsely serrated, the serration little, if any, coarser basally; one or two small symphysial teeth. Lower teeth narrow, erect near the symphysis but slightly oblique laterally, abruptly tapered towards their tips; at the center of the mouth the distal halves of the teeth have finely serrated margins but the basal halves are smooth margined, whereas towards the corners of the mouth the serrations extend more onto the bases of the teeth and are complete in the outermost series; one, two, or occasionally three small symphysial teeth.

First dorsal fin high at all stages of growth but proportionately highest in half-grown specimens (Fig. 72), its apex broadly rounded; origin of first dorsal slightly anterior to inner (posterior) corner of pectoral fin but noticeably nearer to that level than to level of pectoral axil. Second dorsal fin rather high and long, almost equal to anal fin; length of second dorsal rear tip 1.0-1.2 (mean 1.2) times second dorsal height in nine specimens; origin of second dorsal usually just anterior to anal fin origin but exceptionally it may be anterior by a distance equal to almost half the anal base; both second dorsal and anal are placed far back on the caudal peduncle, so that the anal rear tip reaches almost or quite to the origin of the lower lobe of the caudal fin. Pectoral fins noticeably long, especially in half-grown specimens (Fig. 72), only slightly tapered, with broadly rounded tips in small specimens, but slightly angular tips in adults; origin of pectorals below and between the levels of the third and fourth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches almost or quite to level of first dorsal rear tip in small specimens and in large adults, but slightly behind the tip in specimens that are about half grown.

Color in life has variously been described as gray, deep gray, or even greenish blue above, pale to white below, usually with some or all of the fin tips white or mottled white and in some cases splotched or marked with black. After preservation in alcohol the color is grayish brown above, extending down the sides and partly onto the undersurface where the median region is pale; the transition from the grayish brown sides to the pale undersurface is usually mottled. Apex of first dorsal fin, tips of caudal lobes, and tip of pectoral fin on upper side usually pale to white, mottled with grayish brown; sometimes other fins similarly white tipped and mottled; undersides of pectoral and pelvic fins often heavily mottled with brown. In late embryos and subadults some or all of the fins are black tipped or carry black splotches (see Maul 1955:12, fig. 9, and Bass et al. 1973, fig. 19 for examples); the apices of the second dorsal and anal fins, the outer corners of the pelvic fins, and the tip of the ventral lobe of the caudal are prominently black marked; strong black marks are similarly present at the axil of the second dorsal fin and surrounding the upper precaudal pit and may also be present on the back between the dorsal fins; narrow black margins or spots may occur on the apex and anterior margin of the first dorsal, the upper (anterior) margin and terminal lobe of the caudal fin, and the outer tip of the underside of the pectoral; in larger specimens these black markings fade or diminish, and in adults are usually lacking.

Table 73.—*Carcharhinus longimanus*, proportional dimensions in percentage of total length.

	♂ 510 mm east of Florida USNM 118459	♂ 580 mm Hawaiian Is. between Molokai and Oahu USNM 62465	♂ 600 mm Hawaiian Is. between Molokai and Oahu SU 12788	♀ 1,176 mm Sierra Leone BMNH 78.1.24.1	♂ 1,350 mm South Africa Port Eliza- beth	♀ 1,353 mm south of Clipperton Island UCLA 55-304	♂ 1,556 mm Indo- Pacific USNM 197437	♀ 1,670 mm Indo- Pacific USNM 197423	♂ 1,980 mm east of Florida USNM 196132	♂ 2,130 mm Hawaiian Is. Oahu USNM 50859
Snout tip to										
outer nostrils	2.7	3.1	2.8	2.5	3.0	2.6	2.6	2.6	2.6	2.4
eye	6.6	7.1	7.0	5.9	6.3	6.2	6.0	5.9	6.1	5.7
mouth	6.8	6.6	6.7	5.7	6.4	6.2	6.4	6.1	5.9	5.4
1st gill opening	18.0	19.0	19.0	18.1	17.3	18.5	17.6	17.1	16.4	15.7
3d gill opening	20.6	21.0	21.5	21.3	—	20.5	20.4	19.5	19.3	—
5th gill opening	22.3	22.9	23.3	23.0	22.1	22.3	22.0	21.4	20.9	19.2
pectoral origin	21.5	21.5	22.3	21.5	19.3	21.3	20.2	20.1	20.2	17.8
pelvic origin	49.2	50.3	51.8	50.8	50.3	49.8	50.8	50.6	49.9	—
1st dorsal origin	32.0	30.9	31.6	30.9	32.0	29.1	31.5	31.0	30.4	—
2d dorsal origin	61.0	—	61.7	62.2	62.2	60.6	61.5	61.7	60.9	—
anal fin origin	62.0	—	62.7	62.7	62.9	61.3	63.3	62.8	60.9	—
upper caudal origin	71.6	72.8	71.5	72.2	70.4	70.6	71.8	71.3	72.0	—
lower caudal origin	70.0	72.0	70.8	71.5	—	69.3	71.0	70.4	70.9	—
Nostrils										
distance between inner corners	6.1	5.5	6.2	5.6	5.2	5.7	5.8	5.6	6.1	5.2
Mouth										
width	8.4	7.6	8.1	8.1	9.8	8.6	9.8	9.4	8.5	8.3
length	4.9	5.5	5.2	5.2	4.9	4.7	4.5	4.6	4.8	4.5
Labial furrow lengths										
upper	0.4	0.4	0.5	0.6	—	0.4	0.6	0.5	0.5	0.3
lower	0.5	0.4	0.5	0.7	—	0.6	0.6	0.5	0.6	0.6
Gill opening lengths										
1st	2.7	2.6	3.0	2.7	4.0	3.0	3.0	3.9	3.2	2.6
3d	3.0	3.2	3.5	3.7	—	3.1	3.5	4.1	3.7	3.2
5th	2.0	2.2	2.4	3.0	2.8	2.4	3.1	3.0	2.5	2.0
Eye										
horizontal diameter	2.5	2.2	2.2	1.6	1.0	1.4	1.3	1.3	1.2	0.9
1st dorsal fin										
length of base	10.8	12.4	11.3	11.1	11.9	11.5	11.0	10.4	10.5	9.6
length posterior margin	3.3	3.4	3.3	4.4	5.5	5.5	5.2	5.1	4.2	3.3
height	9.2	10.5	9.5	14.3	* 15.2	15.1	13.4	12.9	11.8	11.2
2d dorsal fin										
length of base	4.4	3.6	4.1	4.0	3.7	3.9	4.1	3.7	4.0	3.5
length posterior margin	3.6	3.4	3.3	4.0	3.4	4.5	4.6	4.4	3.8	2.9
height	2.9	2.8	2.7	3.9	* 4.2	3.9	3.6	3.7	3.3	2.8
Anal fin										
length of base	4.1	3.6	4.3	4.7	4.8	4.4	3.9	3.9	5.2	3.2
length posterior margin	3.1	3.1	3.1	3.7	3.9	4.1	4.0	3.9	3.6	3.3
height	3.5	2.9	3.1	4.5	* 5.1	4.5	4.2	4.1	3.5	3.7
Pectoral fin										
length of base	6.7	6.4	7.0	7.2	6.7	6.9	6.9	7.2	6.9	6.7
length anterior margin	22.5	24.2	23.5	26.4	27.1	26.4	25.6	24.3	23.0	20.2
length distal margin	14.9	16.4	15.8	23.2	24.3	24.0	23.1	21.8	19.4	17.4
greatest width	—	—	10.8	11.6	—	12.3	12.4	11.9	11.1	—
Pelvic fin										
length of base	5.7	5.2	5.3	5.6	5.9	5.3	5.8	5.6	5.0	4.4
length anterior margin	7.1	7.6	7.1	8.1	7.7	7.2	7.6	7.7	6.3	5.3
length distal margin	5.5	4.6	4.8	7.0	5.1	6.8	6.4	6.9	5.9	4.9
length of claspers	—	2.2	—	—	—	—	3.6	—	8.9	7.0
Caudal fin										
length of upper lobe	28.1	26.0	27.5	28.8	31.3	29.6	29.6	29.3	28.3	27.2
length of lower lobe	12.9	13.8	12.0	14.2	15.5	15.0	15.4	15.7	13.9	—
Trunk at pectoral origin										
width	12.3	11.6	12.8	11.3	—	12.5	—	12.8	11.6	—
height	11.0	11.6	11.0	12.3	—	—	—	—	11.4	—
Dental formula	—	—	—	—	14-2-14 14-1-14	—	14-2-14 14-2-14	14-2-14 14-1-14	—	14-2-14 14-2-14
Vertebrae										
precaudal		126	125			128				
caudal		110	106			110				
total		236	231			238				

¹This embryo is one of a litter of seven which were part of the original material of *Carcharias insularum*; two (SU 12788 and 12789) of the seven embryos were designated as paratypes by Snyder in the original description.

²Paratype of *Carcharias insularum* (see footnote 1 above).

³Holotype of *Pterolamiops magnipinnis*; dimensions given here are from Smith (1958a) and some of them, particularly those marked by an asterisk, were taken in a different manner to that used in this study, and hence are not strictly comparable.

⁴Holotype of *Carcharias insularum*, a partly skinned out specimen, hence some measurements are of doubtful accuracy.

Vertebral counts of three specimens are given in Table 73 and of another seven specimens in Table 74. Precaudal counts ranging from 123 to 131 (mean 126.8) and total counts of 228-237 (mean 234.4) were given for 14 specimens from the east coast of southern Africa by Bass et al. (1973).

Table 74.—Vertebral numbers in seven specimens of *Carcharhinus longimanus*.

Specimens		Precaudal	Caudal	Total
USNM 52641	Hawaiian Islands	125	108	233
USNM 39078	east of Florida ¹	125	106	231
USNM 39078	east of Florida ¹	125	106	231
USNM 39078	east of Florida ¹	125	108	233
USNM 39078	east of Florida ¹	125	110	235
	W. Africa,			
	1°42'N, 7°51'E ²	126	109	235
	W. Africa,			
	1°42'N, 7°51'E ²	125	97 +	222 +
Range (including counts from Table 73)		125-128	106-110	231-238

¹Sibling embryos.

²Counts supplied by G. Krefft, Institut für Seefischerei, Hamburg 50, Palmalle 9, West Germany, pers. commun. October 1966.

Centrum diameter considerably greater than centrum length even in longest monospondylous centra. Diplospondylous centrum length regular. Diplospondyly begins above anterior third to middle of pelvic base. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.47-0.59 (mean 0.54) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.08-1.33 (mean 1.27) in seven specimens.

The smallest free-living specimen I have seen was 1,176 mm TL, but this is not indicative of size at birth for I have examined embryos up to 600 mm long which from their appearance were almost full term. Bigelow and Schroeder (1948) suggested that young were born at about 650-700 mm in the western North Atlantic, and Bass et al. (1973) estimated birth size at possibly 600-650 mm for their southern African material. Of the few males examined by me, one of 1,556 mm was immature, with a clasper length of 3.6% TL, while two others of 1,980 and 2,130 mm were mature with claspers of 8.9 and 7.0%. Bass et al. (1973) reported that males mature at 1,980 mm off southern Africa, which is a greater size than in central Pacific males as evidenced by data provided by D. W. Strasburg (see footnote 16) on five mature males, the smallest of which was only 1,745 mm.

Rather more information is available on size at maturity and reproduction in the female. Bigelow and Schroeder (1948) recorded a female of 2,070 mm off Cuba which had six embryos, 550-580 mm long, and noted that another litter from off the Bahamas had numbered nine individuals. Krefft (1954) provided data on two pregnant females from off Ecuador in November; one of these, 1,800 mm long, contained seven embryos (one 383 mm long), and the other of 2,300 mm contained only one embryo of 271 mm. Backus et al. (1956) noted that in their material from the western North Atlantic a sample taken from 23 February to 23 March 1954, included six females 1,730-1,980 mm (mean 1,883 mm) long, which, from the appearance of their oviducts, were nulliparous, six others 1,890-2,410 mm (mean 2,132 mm) which were pregnant, and eight others 1,920-2,460 mm (mean 2,212 mm) long which were not pregnant but had previously borne young. From these and other data they suggested that females first mate at a length of about 2,000 mm in the late spring or early summer, that the gestation period is about 1 yr, and that young are born every second year. Their data show that in 16 litters the number of embryos per litter ranged from 1 to 9 with an average of 5.5. There was a good correlation between the length of the mother and the number of embryos she bore, "... the greater the length, the greater the number of pups" (Backus et al. 1956). Strasburg (1958) reported that of 32 female white-tips, all from the equatorial central Pacific except for one from Hawaii, 29 contained no young and ranged in length from 990 to 2,460 mm; about one-fourth of these "infertiles" were as large or larger than the three pregnant females he found; the latter were 1,950, 1,960, and 2,100 mm TL and contained seven, five, and six embryos, respectively. The embryos were rather small (less than 400 mm) at all times of year, hence these "... data suggest a rather different developmental picture from that noted by Backus et al. (1956). ..." (Strasburg 1958). Gohar and Mazhar (1964) noted that of two pregnant females taken in the Red Sea in early April, one of 2,390 mm contained 10 embryos 420-450 mm long, while the other of 2,450 mm had 15 embryos of 520-560 mm. Fourmanoir (1961, as *magnipinnis*) found almost full-term embryos in two females of 2,400 mm taken at the Comoro Islands at the end of September, and suggested that sexual maturity was reached at a length of about 2,250 mm. In the same account (as *budkeri*) he listed a female of 2,630 mm from off Madagascar which contained 19 fertilized eggs in September. The above data from Gohar and Mazhar and from Fourmanoir on embryo or egg numbers and size of mother extend the data given in graphical form by Backus et al. (1956) which indicated that with increasing length of mother there is an increase in the number of young per litter. Bass et al. (1973) noted that females from southern Africa became mature at lengths from 1,800 to 1,900 mm. They reported five pregnant females with six to eight embryos (mean seven) and gave data on embryo size versus month of year; they suggested that the gestation period is about 1 yr, and that the white-tip "... probably mates and gives birth in the spring or early summer. ..."

The largest specimens measured by me were far from maximum size, being only 1,750 and 2,130 mm long for a female and male. Backus et al. (1956) reported that in a sample of 110 white-tips from the western North Atlantic there were very few which exceeded 2,500 mm TL, and the largest was 2,570 mm. This is in accord with other recent accounts where the maximum lengths of specimens were given as follows: Krefft (1954)—3,000 mm in a sample of 47 specimens from off Ecuador and Peru; Strasburg (1958)—2,460 mm female from a small sample of the 1,187 white-tips he discussed from the central Pacific; Fourmanoir (1961)—2,630 mm female from off Madagascar; Gohar and Mazhar (1964)—2,450 mm female from the Red Sea; and Bass et al. (1973)—2,450 mm male (but given as 2,650 mm in their Study Material) and 2,700 mm female from off southern Africa. Earlier accounts of larger specimens, e.g., Bigelow and Schroeder (1948) who noted that there is a literature record of a white-tip measured at 3,500 mm, and who believe that lengths of

up to 3,950 mm are likely, are regarded by Backus et al. (1956) and Springer (1960) as being based on "abnormal" individuals, apparently always females, which continue growing after maturity.

Distribution (see also Material examined).—Bigelow and Schroeder (1948) commented on the remarkable lack of information on white-tips, and concluded that apart from the Hawaiian *insularum* Snyder (which they regarded as distinct) the only verifiable records were from the tropical and subtropical Atlantic, including the Mediterranean. Since that comment there has been, relatively, an explosion of records from widely separate areas, and sufficient information has appeared to show that not only is the white-tip found worldwide, except perhaps for the Mediterranean, but also that it "... is probably the most abundant warm-water pelagic shark" (Strasburg 1958). The more important of these records (most of them as *longimanus*) are as follows: Schuck and Clark (1951) on a specimen from far north (lat. 40°40'30"N) in the western Atlantic; Hubbs (1951) on an east-central Pacific specimen identified from a photograph; Wheeler (1953) on a specimen taken during the Mauritius-Seychelles Fisheries Survey; Krefft (1954) on 47 specimens off Ecuador and Peru; Mather and Day (1954) on 32 specimens from the tropical Atlantic; Maul (1955) on two specimens from Madeira; Backus et al. (1956) on numerous specimens (one of their samples included 110 individuals) from the western North Atlantic; Smith (1958a, as *magnipinnis*) on a specimen from South Africa; Strasburg (1958) on 1,187 specimens from the central Pacific; Fourmanoir (1961, as *magnipinnis* and also as *budkeri*) on 36 specimens from off Madagascar and the Comoro Islands; Tibbo (1962) on a specimen off the Atlantic coast of Canada at lat. 41°01'N; Hess (1962) on 48 specimens from the western North Atlantic; Chen (1963) on two specimens from Taiwan; D'Aubrey (1964) on specimens from off Durban and Lourenco Marques; Gohar and Mazhar (1964) on 21 specimens from the Red Sea; Kato and Carvallo (1967) on three specimens tagged in the eastern Pacific; Krefft (1968) on five specimens from the tropical eastern Atlantic; Sivasubramaniam (1969) on distribution in the tuna fishing grounds of the Indian Ocean; McKay (1970) drawing attention to the record of a specimen taken by a Japanese fisheries training ship in the eastern Indian Ocean; Bass et al. (1973) on 48 specimens from off southern Africa (these authors also refer to numerous other reports from the western Indian Ocean); and Glover (1974) on one specimen from off the southern Australian coast. In addition there are the localities for specimens examined in the present study (see Material examined).

Strasburg (1958) noted that in the central Pacific the range of the white-tip was "... bounded roughly by 20° N. and 20° S. latitude ...". The records given above, plus locality data for specimens which I have examined show that in other regions the white-tip extends at least occasionally into much higher latitudes, e.g., lat. 41°01'N in the western North Atlantic (Tibbo 1962), lat. 40°S (off Argentina) in the western South Atlantic (my data), lat. 39°01'S, below South Africa (Bass et al. 1973), and lat. 35°34'S, off southern Australia (Glover 1974). Attempts to correlate the distribution of the white-tip with physical factors such as temperature and salinity have not been entirely successful, for, as shown by Backus et al. (1956), the white-tip occurs over a wide range of salinities, and they had many records in salinities that could be lower than 28‰, while in respect to temperature the various records in the literature indicate white-tips from a range of 11.1° to 28.0°C. Despite this wide range, the white-tip is a "... warm-water species usually found in water of 21°C or warmer" (Bass et al. 1973). Backus et al. (1956) concluded that within the known latitudinal limits of its range "... white-tips are ordinarily present in the surface waters where depths exceed 100 fathoms [183m], but that they occasionally move into the adjacent shallower water. We suggest that the controlling factor is competition for food with other species of sharks which places the relatively slow-moving white-tip at a disadvantage." Strasburg's (1958) discussion of white-tip distribution arrived at essentially the same conclusions.

The question of whether the white-tip occurs in the Mediterranean is not yet resolved. The 19th century literature contains several reports (under the name *lamia*) suggesting that the white-tip is in that ocean (see Bigelow and Schroeder 1948) but these are not supported by museum specimens, nor have there been any more recent, definite reports. Although this does not establish its absence, as proposed by Tortonese (1951b), it does mean that judgment on its presence must be reserved.

Material examined.—ZSZM (uncat.), two embryos, male, 268 mm, and female, 382 mm, Ecuador, 01°35'S, 81°46'W, 15 November 1951, *Olympic Challenger*; ISZZ 9804, two embryos, female, 292 mm, and male, 300 mm, Pacific Ocean, *Gazelle*; ISZZ 10735, embryo, Hong Kong, Gerlach; ZSZM 14155, two female embryos, 295 and 303 mm, Lesser Antilles, Martinique, 22 November 1911, R. Böhme; ISZZ 4465, female embryo, ca. 300 mm, Atlantic Ocean, Bloch; MNHN 1138, female embryo, 322 mm, India, Coromandel; NMV 61-381 and 61-393, seven embryos, five males, 365-540 mm, and two females, 390 and 395 mm, eastern Pacific, 2°S, 109°W, 1893; ZSZM (uncat.), two embryos, female, ca. 400 mm, and male, 404 mm, western Atlantic, 40°S, 52°W, 1 March 1913, R. Niethe; ISZZ 10148, female embryo, 410 mm, central Atlantic, 5°N, 20°W, Godeffroy; ZSZM 14620, male embryo, 425 mm, Philippine Islands, Mindanao, 4 June 1912, E. Horn; NMV 61-366 and 61-367, two embryos, 480 and 485 mm, Atlantic Ocean; UZMK PO678, embryo, 490 mm, West Indies, Steenburg; ZSZM 12703, female embryo, 505 mm, central Atlantic, 5°N, 20°W, 1886; USNM 118459, two female embryos, 510 and 525 mm, E of central Florida, 28°40'N, 78°46'W, 3 May 1886, *Albatross*; ZSZM 2498, male embryo, 515 mm, central Atlantic, 5°N, 20°W, 1877, Museum Godeffroy; MNHN 1137, female embryo, 520 mm, *Bonite*; USNM 39078, four embryos, two females, 520 and 530 mm, and two males, 520 and 537 mm, E of central Florida, 28°40'N, 78°46'W, 3 May 1886, *Albatross*; USNM 118458, two male embryos, 520 and 530 mm, E of central Florida, 28°40'N, 78°46'W, 3 May 1886, *Albatross*; ZSZM (uncat.), female embryo, 535 mm, Samoa, Apia, Demandt; RNH 11322, female embryo, 545 mm, central Atlantic, 5°N, 20°W, Godeffroy; IFAN 51-1365, female embryo, 570 mm, Aves Islands (Leeward Islands), 30 March 1951, J. Cadenat; UZMK PO680, embryo, 577 mm, western Pacific, 15°N, 143°30'E, 5 May 1874, Corneliusen; USNM 62470, 62465, and 62457, one female and two male sibling embryos, 577, 580, and 580 mm, respectively, from same litter as SU 12788 below, Hawaiian Islands, between Molokai and Oahu, 24 July 1902, *Albatross*; USNM 52641 female embryo, ca. 580 mm, Hawaiian Islands, 28°31'N, 141°47'W, 19 March 1902, *Albatross*; UZMK PO679, embryo, 595 mm, western Pacific, 15°N, 143°30'E, 5 May 1874, Corneliusen; SU 12788, female embryo, 600 mm (paratype of *Carcharias insularum*), Hawaiian Islands, between Molokai and Oahu, 24 July 1902, *Albatross*; BMNH 78.1.24.1, female, 1,176 mm, Sierra Leone, *Challenger*; DIRU 5A, skin of female, 1,350 mm (holotype of *Pterolamiops magnipinnis*), Africa, Port Elizabeth; UCLA 55-304, female, 1,353 mm, South of Clipperton Island, 9°56'N, 109°59'W, 9 October 1955, Scofield; SIO 59-348, male, ca.

1,420 mm, Marshall Islands, Bikini Lagoon, November 1952; USNM 197922, 1,537 mm, Indian Ocean, 19°24'N, 92°31'E, 6 April 1963, *Anton Bruun*; USNM 197437, male, 1,556 mm, Indian or Pacific Oceans; USNM 197423, female, 1,670 mm, Indian or Pacific Oceans; RNH 2544, mounted skin of female, ca. 1,750 mm; USNM 196132, mature male, 1,980 mm, east of northern Florida, 29°57'N, 79°57'W, 4 May 1961, *Silver Bay*; RNH 2519, mounted skin of male, 1,990 mm, Temminck; USNM 50859, skin of mature male, 2,130 mm (holotype of *Carcharias insularum*), Hawaiian Islands, Oahu, off Diamond Head, 28 March 1902, *Albatross*.

Also jaws at several institutions including IFAN, ORID, USNM, and as follows: SAMC 22935, South Africa, 40 mi W of Slangkop, 17 February 1960; SAMC 22949, South Africa, NNE of Cape Recife, 22 April 1960, B. J. Wolmarans; SIO 61-137, western Pacific, 7°10'S, 127°22'E; SIO 54-142, eastern Pacific, 22°10'30"N, 115°12'W; SIO 54-150, eastern Pacific, 25°32'N, 116°42'W; SIO 54-253, eastern Pacific, 22°13'N, 116°27'W; SIO 61-159, central Pacific, 4°20'30"S, 149°30'W.

Also data sheets giving measurements of 21 specimens from the central Pacific taken during the Pacific Oceanic Fishery Investigations reported on by Strasburg (1958).

Also photographs at ORID of eight specimens taken off Durban.

Carcharhinus falciformis (Bibron in Müller and Henle, 1841)

Figures 73, 74

Carcharias (Prionodon) falciformis Bibron in Müller and Henle, 1841:47-48. Type not specified but measurements are given of one specimen from Cuba ascribed to "De la Sagra"; Dumeril (1865:375) notes later that "Le type du Musée de Paris, long de 0m.53, y a été déposé par M. Ramon de la Sagra."

Carcharias (Prionodon) menisorrh Valenciennes in Müller and Henle, 1841:46-47, pl. 17, 19. Seven specimens listed as follows: 1 mounted skin—Berlin Museum; 2 mounted skins—Leiden Museum; 1—British Museum; 1 embryo—Zoological Society Museum; 1—Military Medical Museum in Chatham; 1 mounted skin—Paris; Java, Neuholland (= Australia), Red Sea.

Squalus tiburo Poey, 1860:331-335, pl. 19, figs. 1, 2. Description of female, 880 mm, and comments on other specimens including embryos and males, Cuba.

Aprionodon sitankaiensis Herre, 1934:11-12. Female embryo, stated to be 380 mm long but this was length to upper caudal origin; total length is 528 mm; Philippines, Sulu Archipelago, Sibutu Islands, Sitankai.

Carcharhinus floridanus Bigelow, Schroeder and Springer, 1943:69-74, pls. 13,14. Holotype, female, 2,414 mm, from Fort Pierce, Fla., also jaws, fins, photographs, and measurements of female, about 2,425 mm, from Cochinos Bay, Cuba.

Eulamia malpeloensis Fowler, 1944:299-300, text figs. 7-9. Holotype, embryo, 590 mm, Malpelo Islands, eastern Pacific; paratype, embryo, 556 mm, same locality as holotype; also notes on color of six embryos, 840 mm.

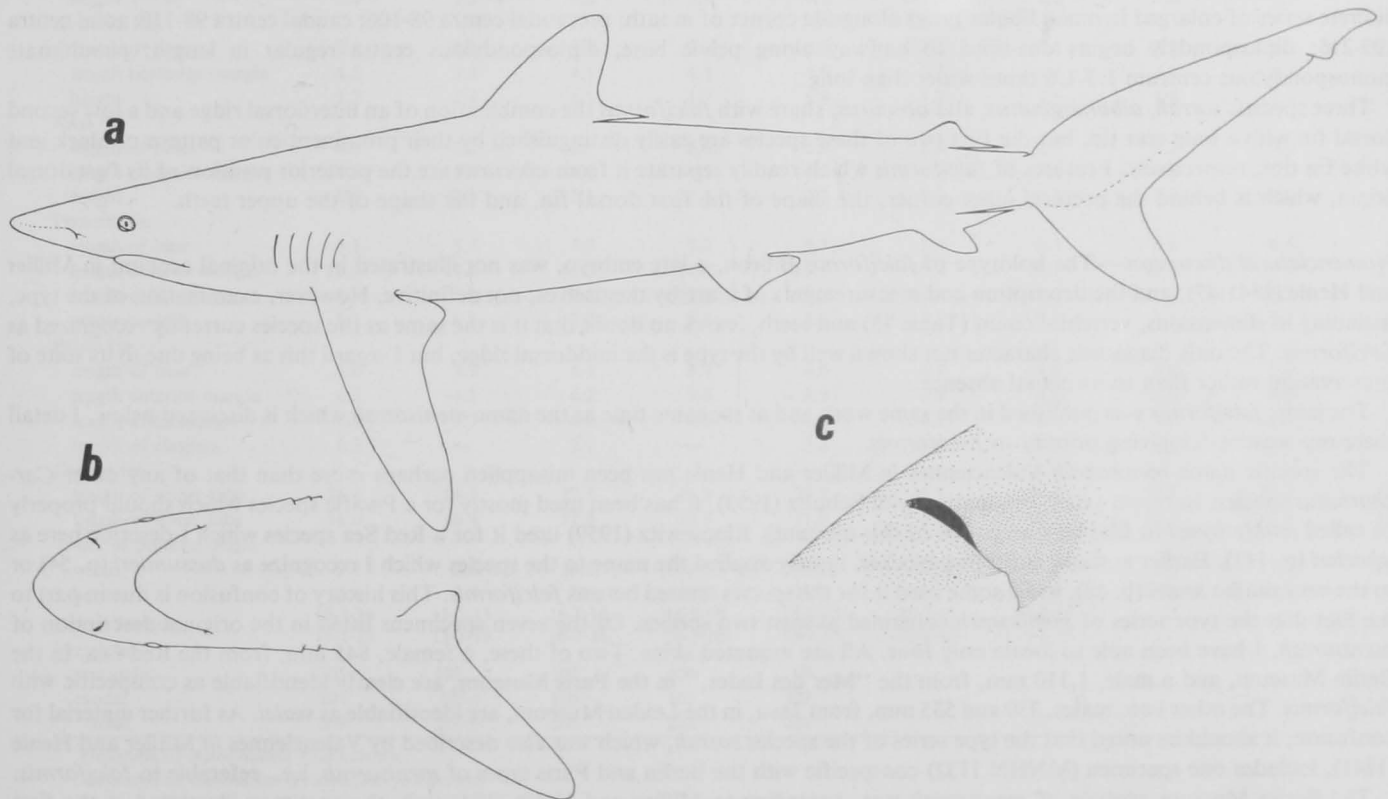


Figure 73.—*Carcharhinus falciformis*, USNM 196791, 1,820 mm TL, female from Guatemala: a, left side; b, underside of head; c, enlarged left nostril.

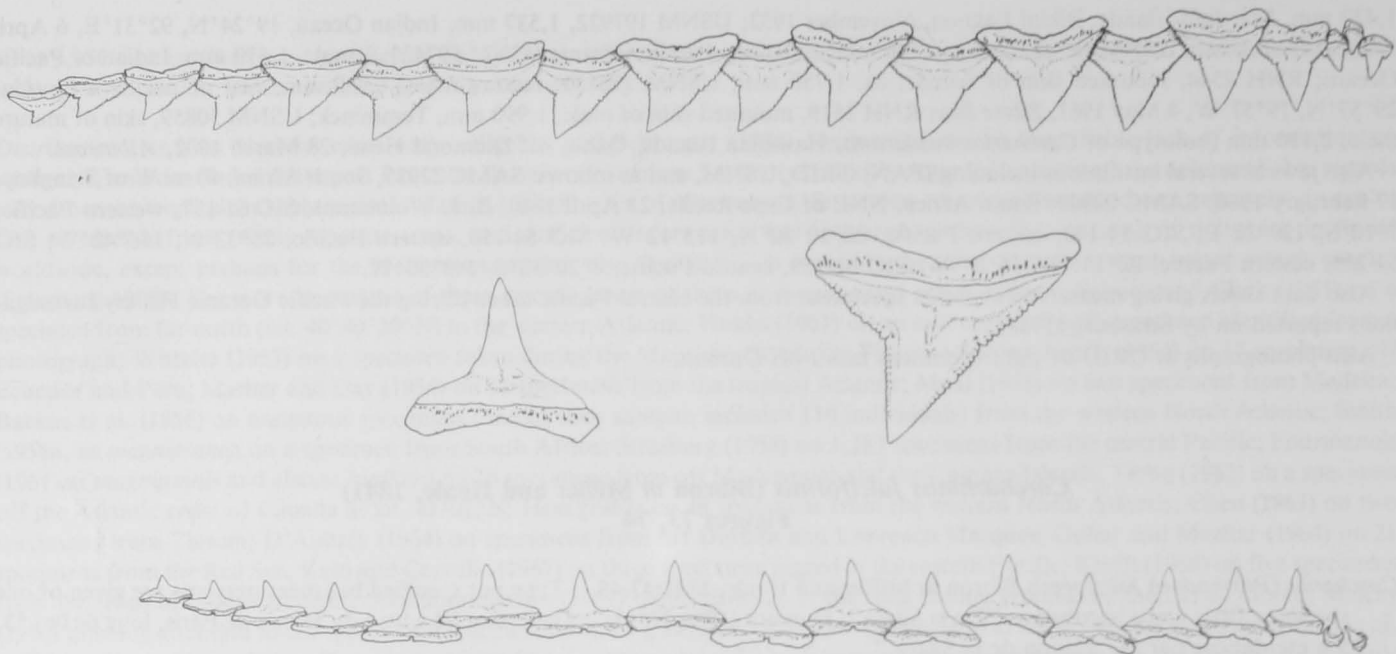


Figure 74.—*Carcharhinus falciformis*, UCLA 59-294, from Pacific Mexico: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

Diagnosis.—Large sharks, up to 3.30 m long, with a low, narrow interdorsal ridge; tips of fins except first dorsal frequently dusky but not black; snout moderately long and bluntly pointed; internarial width 1.2-1.6 in preoral length; origin of first dorsal fin behind inner pectoral corner by not less than one-third the length of inner pectoral margin; apex of first dorsal bluntly pointed or sharply rounded; origin of second dorsal over or usually slightly behind anal fin origin; height of second dorsal 1.3-2.2% TL and 1.6-3.0 in length of its rear tip; dental formula usually $\frac{15-2-15}{15-1-15}$ but may be $\frac{14 \text{ to } 16-1 \text{ to } 3-14 \text{ to } 16}{14 \text{ to } 17-1 \text{ to } 3-14 \text{ to } 17}$; upper teeth moderately broad, oblique, strongly notched laterally and weakly notched medially, with slightly coarser serrations basally; lower teeth erect, smooth edged; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 98-106; caudal centra 98-110; total centra 199-216; diplospondyly begins one-third to halfway along pelvic base; diplospondylous centra regular in length; penultimate monospondylous centrum 1.3-1.6 times wider than long.

Three species, *sorrah*, *albimarginatus*, and *obscurus*, share with *falciformis* the combination of an interdorsal ridge and a low second dorsal fin with a long rear tip, but the first two of these species are easily distinguished by their prominent color pattern of black and white fin tips, respectively. Features of *falciformis* which readily separate it from *obscurus* are the posterior position of its first dorsal origin, which is behind the pectoral inner corner, the shape of the first dorsal fin, and the shape of the upper teeth.

Nomenclatural discussion.—The holotype of *falciformis* Bibron, a late embryo, was not illustrated in the original account in Müller and Henle (1841:47), and the description and measurements of it are by themselves, not definitive. However, examination of the type, including its dimensions, vertebral count (Table 75) and teeth, leaves no doubt that it is the same as the species currently recognized as *falciformis*. The only diagnostic character not shown well by the type is the middorsal ridge, but I regard this as being due to its state of preservation rather than to its actual absence.

The name *falciformis* was published in the same work and at the same time as the name *menisorrah* which is discussed below. I detail there my reasons for giving priority to *falciformis*.

The specific name *menisorrah* Valenciennes in Müller and Henle has been misapplied perhaps more than that of any other *Carcharhinus* species. In recent years, originating with Schultz (1953), it has been used mostly for a Pacific species which should properly be called *amblyrhynchos* Bleeker (see p. 106 of this account). Klauswitz (1959) used it for a Red Sea species which I describe here as *wheeleri* (p. 111). Earlier authors, including Bleeker, mostly applied the name to the species which I recognize as *dussumieri* (p. 54) or to the very similar *sealei* (p. 48), while some used it for the species treated here as *falciformis*. This history of confusion is due in part to the fact that the type series of *menisorrah* contained at least two species. Of the seven specimens listed in the original description of *menisorrah*, I have been able to locate only four. All are mounted skins. Two of these, a female, 845 mm, from the Red Sea, in the Berlin Museum, and a male, 1,110 mm, from the "Mer des Indes," in the Paris Museum, are clearly identifiable as conspecific with *falciformis*. The other two, males, 330 and 535 mm, from Java, in the Leiden Museum, are identifiable as *sealei*. As further material for confusion, it should be noted that the type series of the species *sorrah*, which was also described by Valenciennes in Müller and Henle (1841), includes one specimen (MNHN 1132) conspecific with the Berlin and Paris types of *menisorrah*, i.e., referable to *falciformis*.

The Berlin Museum syntype of *menisorrah* was, according to Müller and Henle (1841:xxi), the specimen illustrated in the first description of the species. I select this specimen as lectotype of *menisorrah*. In so doing this makes the name *menisorrah* synonymous with *falciformis*. Because *menisorrah* and *falciformis* were published simultaneously, it is necessary that one be given priority. The ac-

Table 75.—*Carcharhinus falciformis*, proportional dimensions in percentage of total length.

	♂ embryo 528 mm Philippine Is. Sulu Arch. SU 13601	♀ embryo 528 mm Cuba MNHN 1134	♂ embryo 567 mm Hawaiian Is. Honolulu ANSP 73191	♀ 705 mm eastern Pacific Costa Rica UCLA 55-307	♂ 935 mm Madagascar MNHN 1132	♂ 1,192 mm Florida USNM 196528	♂ 1,500 mm Florida USNM 196529	♂ 1,655 mm Gulf of Mexico Louisiana USNM 197363	♀ 1,820 mm Guatemala Champerico USNM 196791	♀ 2,070 mm Guatemala Champerico USNM 196796
Snout tip to										
outer nostrils	4.7	4.3	4.4	4.8	4.1	4.3	3.7	3.7	4.1	4.0
eye	8.5	7.2	8.6	8.9	7.9	7.5	6.9	6.9	7.8	7.5
mouth	8.5	7.2	8.6	9.1	8.1	7.6	7.1	7.0	7.2	7.4
1st gill opening	19.7	18.7	21.1	21.3	18.6	18.2	18.0	17.6	19.2	20.6
3d gill opening	—	21.3	23.4	—	20.6	20.5	20.1	20.3	21.6	23.7
5th gill opening	24.1	23.4	25.2	25.5	22.7	22.2	22.1	22.3	23.4	25.6
pectoral origin	22.3	22.3	23.8	24.1	21.6	20.5	20.3	21.2	21.7	22.6
pelvic origin	46.8	49.0	48.5	51.8	48.3	48.3	47.2	48.3	49.8	50.1
1st dorsal origin	33.1	32.9	33.9	35.0	32.4	31.9	32.4	30.7	34.3	33.6
2d dorsal origin	64.2	62.8	63.5	64.4	62.7	64.4	63.6	63.5	65.7	64.7
anal fin origin	61.4	62.3	61.7	63.7	62.5	63.9	62.9	63.7	65.0	63.9
upper caudal origin	72.0	72.2	73.0	73.8	72.8	73.8	73.1	73.6	74.6	74.0
lower caudal origin	71.2	71.7	72.0	72.6	71.8	73.2	72.3	73.0	74.2	72.6
Nostrils										
distance between inner corners	6.1	5.4	5.7	6.0	5.4	5.5	5.4	5.3	5.5	5.4
Mouth										
width	8.1	7.8	7.1	8.8	7.5	7.9	7.9	7.5	7.7	7.6
length	5.7	4.7	5.3	5.2	4.6	4.3	4.4	4.2	5.1	5.2
Labial furrow lengths										
upper	0.4	0.5	0.5	0.4	—	0.3	0.4	—	0.5	0.4
lower	0.5	0.4	0.4	0.4	—	0.4	0.4	—	0.5	0.4
Gill opening lengths										
1st	2.8	2.7	—	3.0	3.2	3.1	3.3	2.5	2.4	2.9
3d	3.2	2.9	—	3.3	3.6	3.5	3.5	3.0	2.9	3.4
5th	2.2	2.2	—	2.4	2.5	2.3	2.4	2.1	2.1	2.0
Eye										
horizontal diameter	2.7	2.7	2.6	2.2	1.8	1.5	1.4	1.4	1.2	1.3
1st dorsal fin										
length of base	8.7	8.2	8.3	8.4	8.0	8.4	8.0	9.3	9.0	8.4
length posterior margin	4.2	3.8	4.0	4.1	4.6	3.9	4.0	4.8	4.1	4.3
height	5.9	5.2	6.0	7.1	7.2	7.4	7.2	8.0	7.9	8.1
2d dorsal fin										
length of base	2.8	2.1	2.8	2.8	2.5	2.0	2.1	3.0	2.7	2.6
length posterior margin	4.5	3.8	4.1	4.3	4.9	4.3	4.1	4.7	4.3	—
height	1.7	1.4	1.5	1.7	1.8	1.5	1.6	1.8	1.8	2.1
Anal fin										
length of base	4.0	2.8	3.7	3.0	2.9	2.8	2.8	3.2	3.6	3.6
length posterior margin	4.5	3.9	4.1	4.5	4.9	4.2	4.1	4.8	4.0	4.8
height	2.3	2.1	2.1	2.4	2.2	2.3	2.3	2.3	2.7	2.8
Pectoral fin										
length of base	5.1	5.4	5.6	5.7	5.7	5.9	6.1	5.6	6.5	6.0
length anterior margin	15.9	14.2	15.3	14.9	15.5	15.4	16.3	18.3	20.2	21.7
length distal margin	8.9	7.9	9.2	12.2	12.2	11.4	13.0	13.3	16.5	17.7
greatest width	8.1	6.5	7.7	8.5	8.2	7.6	8.3	8.5	9.7	9.7
Pelvic fin										
length of base	4.0	3.9	4.1	3.7	4.4	4.5	4.5	4.6	5.0	4.6
length anterior margin	4.2	4.3	4.2	3.8	3.9	3.9	4.2	4.8	4.8	5.1
length distal margin	4.2	3.7	4.2	4.5	4.9	4.5	4.6	4.8	5.4	4.8
length of claspers	2.3	—	2.1	—	2.2	1.8	2.3	2.8	—	—
Caudal fin										
length of upper lobe	26.3	26.5	27.5	26.2	27.7	26.1	27.4	27.8	26.7	26.3
length of lower lobe	11.0	10.4	11.5	10.9	11.9	11.5	12.3	12.9	12.6	13.2
Trunk at pectoral origin										
width	9.3	9.8	10.2	11.0	10.3	11.5	11.1	11.8	11.6	11.2
height	10.6	9.3	8.6	10.3	11.8	11.1	10.5	10.6	10.8	9.9
Dental formula	16-1-16 16-1-16	15-2-15 15-1-15	16-1-16 16-1-16	16-2-16 16-1-16	15-1-15 15-1-15	15-2-15 15-1-15	15-2-15 15-1-15	—	—	—
Vertebrae										
precaudal	105	102	102	104	99					
caudal	104	105 +	103	108	102					
total	209	207 +	205	212	201					

¹Holotype of *Aprionodon siankaiensis*.²Holotype of *Carcharias (Prionodon) falciformis*.³Syntype of *Carcharias (Prionodon) sorrah*.

count of *menisorrah* precedes, by one page, that of *falciformis*, but despite this, as first reviser I select the name *falciformis* to have priority. This action provides for the retention of the name *falciformis* which is well established and has not been a cause of confusion. In contrast, the name *menisorrah* becomes a junior synonym, a fate of which it is more deserving in view of the confusion that has surrounded its usage.

Although I have no information as to whether there is any type material of Poey's *tiburo* still remaining, there can be little or no doubt from Poey's description (1860) of the species, and his illustrations of the teeth (pl. 19, figs. 1, 2), that it was *falciformis*. In particular, such features as the shape of the snout, the lack or virtual lack of nostril lobes, the shape and rearward position of the first dorsal fin relative to the pectorals, the nature of the second dorsal and anal fins, viz. "opposées, ses pointes postérieures tres longues," the dental formula and the shape of the teeth all point to *falciformis*. As Bigelow and Schroeder (1948) have commented, Poey himself (1866-68:172) at one stage concluded that *tiburo* was a synonym of *falciformis*, though earlier (1860) and again later (1866-68:499) he regarded them as distinct.

Herre (1934:11) described *sitankaiensis* from one small specimen, 528 mm TL, from the Sulu Archipelago, Philippine Islands. He stated that the teeth were "not serrated," and hence placed *sitankaiensis* in the genus *Aprionodon*. He did not compare it with any other species, and his rather general description is inadequate for identification. The holotype of *sitankaiensis*, deposited at Stanford University (SU 13601), is a late embryo still bearing a yolk stalk. Its upper teeth, contrary to Herre's description, are serrated, though the serrations are few and present mainly on the medial margins; the lateral margins are deeply notched. The lower teeth are smooth, and the dental formula is $\frac{16-1-16}{16-1-16}$ ($\frac{33}{33}$) rather than $\frac{29}{31}$ as given in Herre). The nature of the teeth and their number, together with the proportional dimensions of the holotype and its fin shapes and positions, leave no doubt that *sitankaiensis* is conspecific with *falciformis*. There is, however, little sign of a middorsal ridge, but I believe this lack is an artifact of preservation. A vertebral count of the holotype, kindly provided by L. J. V. Compagno (pers. commun.) further confirms the identification.

The relationship of *floridanus* Bigelow, Schroeder, and Springer to *falciformis* was discussed in detail in Garrick et al. (1964) where it was shown that *floridanus*, based on adult specimens (holotype is skin of adult female, MCZ 35807, seen by me), and *falciformis*, based on an embryo, represent the size extremes of a single species which should be named *falciformis*.

The type specimens of *malpeloensis* Fowler cannot now be found. Both were embryos (holotype, ANSP 70,048, 590 mm; paratype, ANSP 70,049, 556 mm) but Folwer's (1944) description and illustrations of them when compared with specimens of *falciformis* of similar size leave no doubt that they were *falciformis*. In particular, Fowler's description that "First dorsal origin well behind inner end of depressed pectoral angle," and his illustration displaying this feature plus the shape of the first dorsal and the attenuate second dorsal and anal fins, are virtually diagnostic in themselves. The redescription of two subadults, as *malpeloensis*, by Rosenblatt and Baldwin (1958) further substantiates the view that *malpeloensis* is a synonym of *falciformis*.

The uncertain relationship between *falciformis* and *falcipinnis* Lowe, 1839, which latter name predates *falciformis* is discussed on p. 187.

Description (see also Table 75).—Large sharks, growing to 3.3 m TL. Midline of back between dorsal fins with a low, narrow interdorsal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles close-packed, overlapping, subcircular in outline, slightly wider than long, each with three strong longitudinal ridges and corresponding sharp-pointed but short posterior marginal teeth in embryos and juveniles, but with five ridges and teeth in subadults, and seven in larger specimens.

Snout moderately long and bluntly pointed in contour. Anterior margin of eye slightly forward of or above front of mouth in small and subadult specimens but slightly behind front of mouth in larger adults. Nostrils strongly oblique, slitlike, the anterior margin of each almost straight and with a very weakly developed lobe.

Dental formula $\frac{15 \text{ or } 16-1 \text{ or } 2-15 \text{ or } 16}{15 \text{ or } 16-1 \text{ or } 2-15 \text{ or } 16}$ in 23 specimens (up to 1.9 m long) out of 35 (of all sizes) counted by me; 9 specimens (1.0 to about 2.0 m long) of those remaining had similar formulae except for having three symphyseal teeth in either the upper or the lower jaws; while three of the largest specimens (about 2.5 m long) had formulae of $\frac{16 \text{ or } 17-1 \text{ to } 3-16 \text{ or } 17}{16 \text{ or } 17-1 \text{ to } 3-16 \text{ or } 17}$. In large specimens the most

lateral tooth in each jaw was frequently noticeably smaller than the adjacent penultimate tooth and could easily be overlooked. Upper teeth moderately broad, oblique except for the first two or three series on each side of symphysis, their lateral margins strongly notched, their medial margins very weakly notched, both margins serrated, the serrations fine distally on the tooth but coarser and more irregular at the notch and basally; one, two, or three small symphyseal teeth. Lower teeth narrow, erect except for the most lateral series, both margins concave basally, smooth edged; one, two, or three small symphyseal teeth.

First dorsal fin moderately low, its apex rounded and its rear tip relatively long and attenuate; origin of first dorsal definitely behind inner (posterior) corner of pectoral fin by a distance not less than one-third to half the length of the inner (posterior) margin and as much as the length of this margin in some specimens. Second dorsal fin low and long, similar to anal fin but lower and with a concave rather than notched distal margin; length of second dorsal rear tip 1.6-3.0 (mean 2.5) times second dorsal height for 34 specimens; origin of second dorsal over or more often slightly behind anal fin origin, to as far back as anterior third of anal base. Pectoral fins moderately long, slender, with rounded tips; origin of pectorals below the third gill openings or below and between the levels of third and fourth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches from only halfway to two-thirds along first dorsal base in juveniles but extends to the first dorsal axil in subadults and to about two-thirds along the first dorsal rear tip in adults.

Color in life was described by Kato (1964) from eastern Pacific specimens as "Dorsal surface dark brown to dark gray, pectoral fins noticeably darker; sides metallic gray with greenish tinge; ventral surface white, except for dusky to dark tips on the pectoral and pelvic fins; color variant, rarely found, with light mottling over the entire dorsal surface." After preservation in alcohol the color is gray or

blue-gray above, pale to white below; frequently the pectoral, pelvic, second dorsal, and anal fins are dusky tipped but not black. I have also seen specimens in which the upper margin of the caudal fin is dusky.

Vertebral counts of five specimens are given in Table 75 and of another 19 specimens in Table 76. A frequency distribution of precaudal vertebral numbers (Table 77) based on 23 counts from my sample (excluding BMNH 1935.5.2.1-2 from the mid-Atlantic St. Paul's Rocks and USNM 197426 from "Pacific or Indian Oceans") plus 4 counts (102, 105, 105, 106) from Bass et al. (1973) from the southwest Indian Ocean, gives no firm picture of differences between populations.

Centrum diameter considerably greater than centrum length even in longest monospondylous centra. Diplospondylous centra regular in length. Diplospondyly begins above the anterior third to middle of pelvic base. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.64-0.77 (mean 0.70) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.06-1.35 (mean 1.16) in 16 specimens.

Table 76.—Vertebral numbers in 19 specimens of *Carcharhinus falciformis*.

Specimens		Precaudal	Caudal	Total
MCZ 40792	Bermuda	105	110	215
	off N. Carolina ¹	106	104	210
USNM 35643	Delaware	98	101	199
USNM 38509	South Carolina	100	109	209
USNM 196266	Florida	101	108	209
ANSP (uncat.)	Bahamas	101	106	207
SU 52847	Brazil	99	101	200
SU 52849	Brazil	101	105	206
BMNH 1935.5.2.1-2	equat. Atlantic, St. Paul's Rocks	101	105	206
CU 42569	equat. W. Africa	100	99	199
	W. Africa, Guinea ²	99	102	201
	W. Africa, Guinea ²	99	104	203
	W. Africa, Guinea ²	100	109	209
USNM 197426	Pacific or Indian Oceans	104	109	213
ISZZ 7037	New Zealand	105	105	210
SIO 54-250	Baja California	103	101	204
SU 53661	Mexico, Acapulco	104	98	202
SIO 61-428	off Pacific Guatemala	103	102	205
UCLA 56-239	Clipperton Is.	104	105	209
Range (including counts from Table 75)		98-106	98-110	199-215

¹Count supplied by S. Gruber, University of Miami, Marine Laboratory, 1 Rickenbacker Causeway, Miami, Fla., pers. commun. September 1964.

²Counts supplied by G. Krefft, Institut für Seefischerei, Hamburg 50, Palmaille 9, West Germany, pers. commun. October 1966.

Table 77.—Frequency distribution of precaudal vertebral numbers in *Carcharhinus falciformis*.

Ocean	98	99	100	101	102	103	104	105	106
Western Atlantic	1	1	1	3	1			1	1
Eastern Atlantic		2	2						
Indian		1			1			2	1
Pacific					1	2	4	2	

Table 78.—Clasper length as percentage of total length in *Carcharhinus falciformis*.

Total length (mm)	Clasper length (% TL)	Total length (mm)	Clasper length (% TL)
794	2.0	1,500	2.3
842	2.2	1,560	2.4
935	2.2	1,655	2.8
1,030	2.2	1,660	2.6
1,052	1.7	1,750	2.8
1,192	1.8	1,780	2.8
1,390	2.9	1,870	10.9
1,420	2.8	2,465	12.3

Table 79.—Number of embryos per litter, size at birth, size at maturity, and maximum size in *Carcharhinus falciformis*.

Ocean	Embryos per litter		Size at birth (TL mm)	Size at maturity (TL mm)		Maximum size (TL mm)	
	Range	(Mean)		♂	♀	♂	♀
Western North Atlantic							
Springer (1960)	—		700-850	2,170	2,300	2,700	3,050
Gilbert & Schlernitzauer (1965)	6-14(?)		—	—	—	—	—
(1966)	9	n = 1	—	—	—	—	—
Eastern Atlantic							
Bane (1966)	9-12	(10.5) n = 2	—	—	2,375	3,000	
Western Indian							
Fourmanoir (1961)	9-14	(11.0) n = 6	740-780	—	2,480	2,440-2,830	
Bass et al. (1973)	—		780-870	2,400	2,600	—	—
Central Pacific							
Strasburg (1958)	2-11	(6.5) n = 12	—	—	2,130	—	—

The smallest apparently free-living specimen I have seen was 670 mm, while the largest embryo was 625 mm. In my material, maturity in the males, as evidenced by clasper length shown in Table 78, was not reached until 1,870 mm TL.

A reasonably extensive picture of the broad features of the biology of *falciformis* can be constructed from the accounts of Springer (1960) and Gilbert and Schlernitzauer (1965, 1966) for the western North Atlantic, Bane (1966) for the eastern Atlantic, Fourmanoir (1961) and Bass et al. (1973) for the western Indian Ocean, and Strasburg (1958) for the central Pacific. Salient features from these accounts are as in Table 79.

The largest adult specimens reported in the literature are those in Garrick et al. (1964) from the western Atlantic which were up to 3,300 mm long.

Distribution (see also Material examined).—*Carcharhinus falciformis* is a widely distributed tropical-subtropical species in the Atlantic, Pacific, and Indian Oceans. It is pelagic but not restricted to the open ocean, and appears to have a wider latitudinal distribution along continental coastlines than it does farther offshore. Strasburg (1958), in reporting on the capture of 2,176 specimens of *falciformis* from the central Pacific, noted that it is an "... equatorial species, the range ... being practically restricted to a band about 10 degrees (600 miles) on either side of the Equator. . . ." However, specimens I have examined, and literature records subsequent to Strasburg (1958), now give *falciformis* a much wider latitudinal range. Records of *falciformis* (some as *floridanus*) incorporated in the distribution set out below include those of: Kato et al. (1967) and Kato and Carvalho (1967) for the eastern Pacific; Strasburg (1958) and Tester (see footnote 4) for the central Pacific; Bryan (1973) for Guam Island; Fourmanoir (1961), D'Aubrey (1964), and Bass et al. (1973) for the western Indian Ocean; Poll (1951), Cadenat (1957, 1961), Bane (1966), and Krefft (1968) for the eastern Atlantic; and Bigelow and Schroeder (1948), Springer (1960), Garrick et al. (1964), and Cervigon (1968) for the western Atlantic.

On the basis of the above, the distribution of *falciformis* is as follows: a) eastern Pacific from southern Baja California to Peru, including the Revillagigedos, Clipperton, Cocos, and Malpelo Islands; b) central and western Pacific including the Hawaiian Islands, Marshall Islands, Mariana Islands (Guam), Philippine Islands, and New Zealand (the actual proximity to New Zealand not known); c) Red Sea and western Indian Ocean from Zanzibar to at least as far as lat. 26°35'S (southern Mozambique) and including Madagascar and the Comores; d) eastern Atlantic from as far north as Madeira and southwards to the Gulf of Guinea (where it is very common) and to at least lat. 8°29'S; and e) western Atlantic from off Cape Cod in the north to southern Brazil (Espírito Santo, Vitória), including Bermuda, the Gulf of Mexico, and the Caribbean Sea. It is also present in the equatorial mid-Atlantic as evidenced by one specimen (BMNH 1935.5.2.1-2) from St. Paul's Rocks. The principal gap, and one that is unlikely to be real, in an expected circum-tropical distribution is the extensive Indo-Australian region. Sivasubramaniam (1969) reported that *falciformis* forms 75-80% of the pelagic sharks caught off Ceylon; but I have seen no material from that region or southwards to Australia.

Material examined.—ISZZ 7037, female embryo, 430 mm, New Zealand, Salmin; SMNS 3594, female embryo, 435 mm, Red Sea, Koseir, 1894, Klunzinger; UCLA 59-83, male embryo, 460 mm, Mexico, Islas Revillagigedo, Roca Partida, 15 May 1958, *Independence*; BMNH 1935.5.2.1-2, male embryo, 460 mm, and female embryo, 475 mm, equatorial Atlantic, St. Paul's Rocks, *Discovery*; IFAN 62.29, female embryo, 490 mm, French West Africa, 6 September 1961; MNHN 63.3, two female embryos, 490 and 564 mm, Madagascar, Fourmanoir; MNHN 1134, female embryo, 528 mm [holotype of *Carcharias (Prionodon) falciformis*], Cuba, Ramon de la Sagra; SU 13601, male embryo, 528 mm (holotype of *Aprionodon sitankaiensis*), Philippine Islands, Sulu Archipelago, Sibutu Island, 12 August 1931, A. W. C. T. Herre; SIO 48-272, male embryo, 533 mm, Mexico, Baja California, 25 mi NW of Cape San Lazaro; ANSP 73191, male embryo, 567 mm, Hawaiian Islands, Honolulu, 1923, from Bishop Museum; CU 42569, female embryo, 580 mm, equatorial eastern Atlantic, 1°30'S, 8°20'E, 20 August 1961, G. W. Bane; SU 52847, female embryo, 625 mm, Brazil, Espírito Santo, Vitória, 14 December 1944; IRSN (no number), male embryo, 650 mm, Spain, Malaga (from fish market), 20 July 1962, J. P. Gosse; SU 53661, male, ca. 655 mm, Mexico, off Acapulco, December 1959, *Santa Helena*; USNM 196266, female, 670 mm, E of Florida, 25°14'N, 8 July 1961, B. Forsmark; UCLA 55-307, two females, 705 and 1,060 mm, eastern Pacific, S of Costa Rica, 7°24'N, 86°30'W, 1 November 1955, C. Blunt; MRAC 80258, male, 725 mm, West Africa, 1°13'S, 8°31'E, 9 March 1949; IFAN (no number), male, 770 mm, French West Africa, Casamance, April 1962; USNM 38509, male, 794 mm, South Carolina, 33°37'30"N, 77°36'30"W, 20 October 1885, *Albatross*; IFAN 3058, female, 795 mm, Senegal, Goree, 31 August 1946, J. Cadenat; IFAN (no number), male, 800 mm, French West Africa, Casamance, April 1962; IRSN 6.914, female, ca. 800 mm, West Africa, 9°51'N, 15°30'W, 11 January 1938, *Mercator*; USNM 35643, male, 842 mm, Delaware, 39°12'N, 73°11'W, 12 September 1884, *Albatross*; ISZZ 4476, mounted skin of female, ca. 845 mm [syntype of *Carcharias (Prionodon) menisorrah*], Red Sea, Hemprich and Ehrenberg; IRSN 8.401, male, ca. 865 mm, West Africa, 1°13'S, 8°31'E, 9 March 1948, *M'bizi*; MRAC 80259, female, 885 mm, West Africa, 3°05'S, 9°25'E, 25-26 March 1949; SU 52849, female, 895 mm, Brazil, Espírito Santo, Vitória, 2 September 1944; NMV 50088 (old number), female 895 mm, Senegal, Goree, 1880, Steindachner; IRSN 8.402, male, ca. 900 mm, West Africa, 1°01'S, 8°31'E, 3 March 1949, *M'bizi*; BMNH 1871.9.13.252, male, ca. 900 mm, equatorial Atlantic, 2°56'N, 26°31'W, Schmeltz; UMML 9878, two males, 908 and 915 mm, Florida, in Gulf Stream off Miami, December 1961—January 1962, S. Gruber; MNHN 1132, male, 935 mm [syntype of *Carcharias (Prionodon) sorrah*], Madagascar, Quoy and Gaimard; ISZZ 13368, female, 950 mm, West Indies, Kuhfuss; BMNH 1851.4.9.14, mounted skin (no. 840) of male, ca. 950 mm (labelled as probable syntype of *Carcharias falcipinnis*), Madeira, 1839, Lowe; MRAC 80260, male, ca. 1,000 mm, West Africa, 4°57'S, 11°16'E, 35 mi W by S of Point Noire, 28 March 1949; NMV 61.437, female, 1,000 mm, West Africa, Fernando Po, 1885; MCZ 40792, male, 1,030 mm, western Atlantic, NE of Bahamas, 28°24'N, 73°16'W, F. Mather et al.; CNHM 47881, female, 1,032 mm, NW of Yucatan, 10 mi N of Cayo Arenas, 16 August 1951, *Oregon*; ANSP (no number), male, 1,052 mm, Bahamas, Cat Cay, Wahoo Hole, 24 February 1957; MNHN A 9662, mounted skin of male, 1,110 mm [syntype of *Carcharias (Prionodon) menisorrah*], Mer des Indes, Kuhl and Van Hasselt; USNM 197426, female, 1,110 mm, Pacific or Indian Oceans; UMML 6117, female, 1,133 mm, Florida, Dade County, about 2 mi N of sea buoy off Government Cut, Miami, 26 December 1959, J. K. Howard; BMNH 1912.12.10.41, male, 1,175 mm, St. Paul, R. L. Clark; USNM 197370, female, 1,190 mm, Atlantic Panama, Golfo de los Mosquitoes, 9°0'N, 81°26'W, 30 May 1962, *Oregon*; USNM 196528, male, 1,192 mm, off northern Florida, 29°44'N, 80°18'W, 4 October 1961, *Silver Bay*; USNM 197364, two males, 1,390 and 1,660 mm, Gulf of Mexico, 25°39'N, 88°06'W, 26 September 1961, *Oregon*; USNM 197363, three males, ca. 1,420, 1,655, and 1,780 mm, Gulf of Mexico, S of Louisiana, 28°19'N, 90°06'W, 2 September 1961, *Oregon*; USNM 197436, male, 1,475 mm, Pacific or Indian Oceans; USNM 196529, male, 1,500 mm, off northern Florida, 29°44'N, 80°18'W, 4 October 1961, *Silver Bay*; USNM 196530, male, 1,560 mm, off northern Florida, 29°44'N, 80°18'W, 4 October 1961, *Silver Bay*; USNM 197371, male, 1,750 mm, Gulf of Mexico, off Alabama, 29°38'N, 88°15'W, 22 September 1961, *Oregon*; USNM 196791, female, 1,820 mm, Guatemala, Champerico, 14°22'N,

92°48' W, 3 February 1962, Kato et al.; USNM 196820, mature male, ca. 1,870 mm, El Salvador, 12°29' N, 88°57' W, 5 February 1962, Whitney et al.; USNM 220903, female, ca. 1,900 mm, northern Marshall Islands, 1947, J. C. Marr; USNM 196827, female, 1,920 mm, Guatemala, Champerico, 14°22' N, 92°48' W, 3 February 1962, Kato et al.; USNM 196826, female, 1,940 mm, Guatemala, Champerico, 14°22' N, 92°42' W, 3 February 1962, Kato et al.; USNM 196828, female, 1,955 mm, Guatemala, Champerico, 14°22' N, 92°48' W, 3 February 1962, Kato et al.; USNM 196789, female, 1,965 mm, Mexico, Guerrero, 16°50' N, 102°15' W, 29 January 1912, Hugh M. Smith; USNM 196823, female, 2,030 mm, Guatemala, Champerico, 14°22' N, 92°48' W, 3 February 1962, Kato et al.; USNM 196796, female, 2,070 mm, Guatemala, Champerico, 14°22' N, 92°48' W, 3 February 1962, Hester et al.; MCZ 35807, female (partly skinned), ca. 2,300 mm (holotype of *Carcharhinus floridanus*), Florida, Fort Pierce, 2 November 1942; UCLA 56-239, head and tail of female, 2,440 mm, plus embryo from same, ca. 325 mm, eastern Pacific, Clipperton Island, 24 October 1956, Spencer F. Baird; MCZ 40793, jaws, skin sample, photographs, and measurements of mature male, 2,465 mm, W of Bermuda, 27°23' N, 75°04' W, 27 April 1961, Mather et al.

Also, jaws and other fragmentary material of many specimens from various institutions, and particularly at IFAN (Senegal, Goree); radiographs from two small specimens (latter not seen) as follows: SIO 61-428, eastern Pacific, 12°31' N, 91°04' W; and SIO 54-250, Mexico, Baja California.

Also, measurements of seven males and five females, 877-2,270 mm long, taken in the central Pacific during 1952 through 1956 by the Pacific Oceanic Fishery Investigations of the U.S. Fish and Wildlife Service, and supplied by Donald W. Strasburg.

Carcharhinus sorrah (Valenciennes in Müller and Henle, 1841)

Figures 75, 76, 77

Squalus Spallanzani Peron and Lesueur, in Lesueur, 1822:351. No material mentioned; terre de Witt, New Holland = northwestern Australia.

Carcharias (Prionodon) sorrah Valenciennes in Müller and Henle, 1841:45-46, pl. 16. A spirit-preserved specimen in the Leiden Museum, two specimens in the Museum of the Zoological Society of London, a spirit-preserved specimen in Paris from Pondicherry through Bélanger, and a specimen from Madagascar; India, Java, Madagascar.

Carcharias (Prionodon) bleekeri Duméril, 1865:367-368. - Two specimens from Pondicherry through Leschenault.

Carcharias taeniatus Hemprich and Ehrenberg, 1899:8, pl. 4, figs. a, b, c, d, e. No material mentioned, but the main illustration is stated to be of a female, one-third natural size, which would make the specimen 882 mm long; the accompanying figures of the teeth, dermal denticles, underside of head, etc. are said to be from the same specimen, but they include a view of the pelvic fins showing claspers, hence a male must also have been used; Red Sea.

Galeolamna (Galeolamnoides) isobel Whitley, 1947:129-131, text fig. 1. Holotype, female, 910 mm, Western Australia, Long Island, between Cape Preston and the Mary Anne Group.

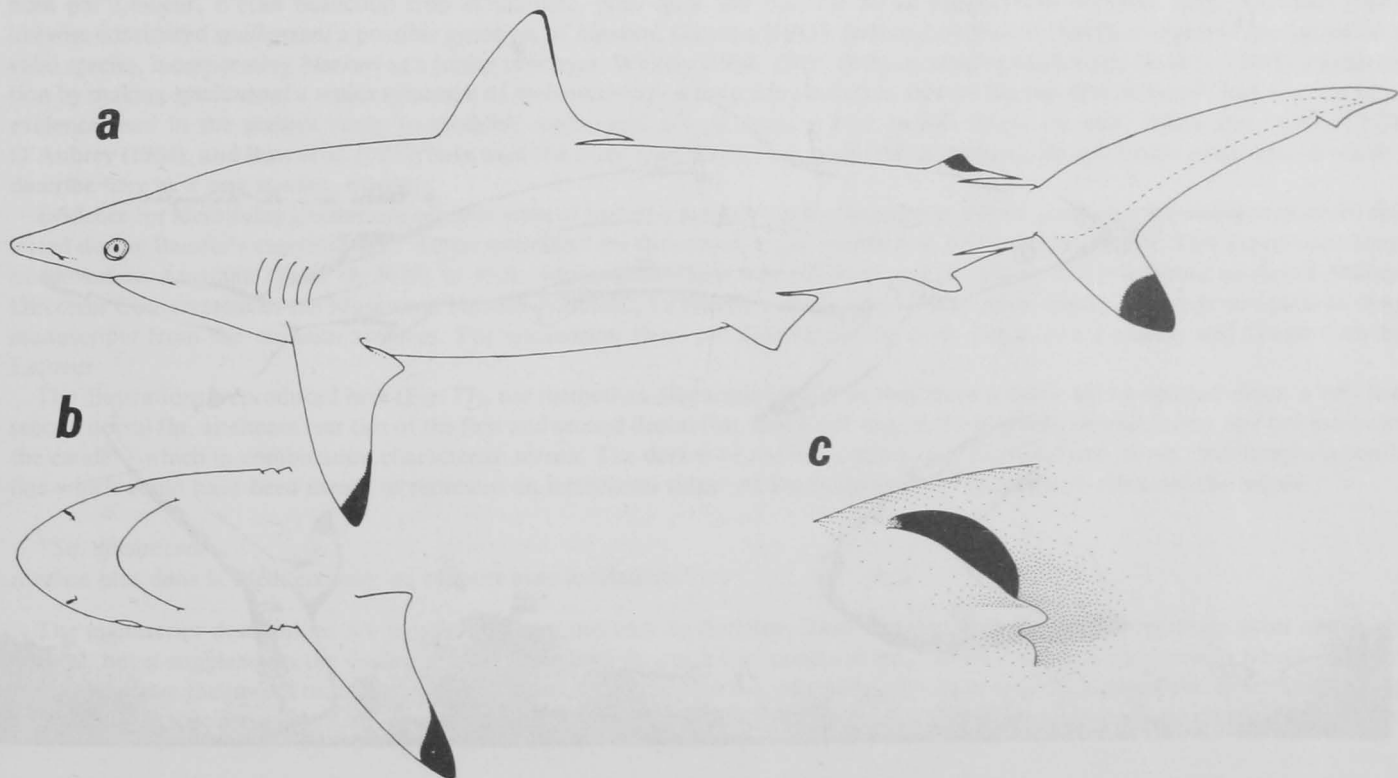


Figure 75.—*Carcharhinus sorrah*, GVF 2467, 1,266 mm TL, female from Gulf of Thailand: a, left side; b, underside of head; c, enlarged left nostril. Note: Dark markings on fins not recorded when specimen was drawn but were added subsequently using Bass et al.'s (1973) figure 29 as a basis.

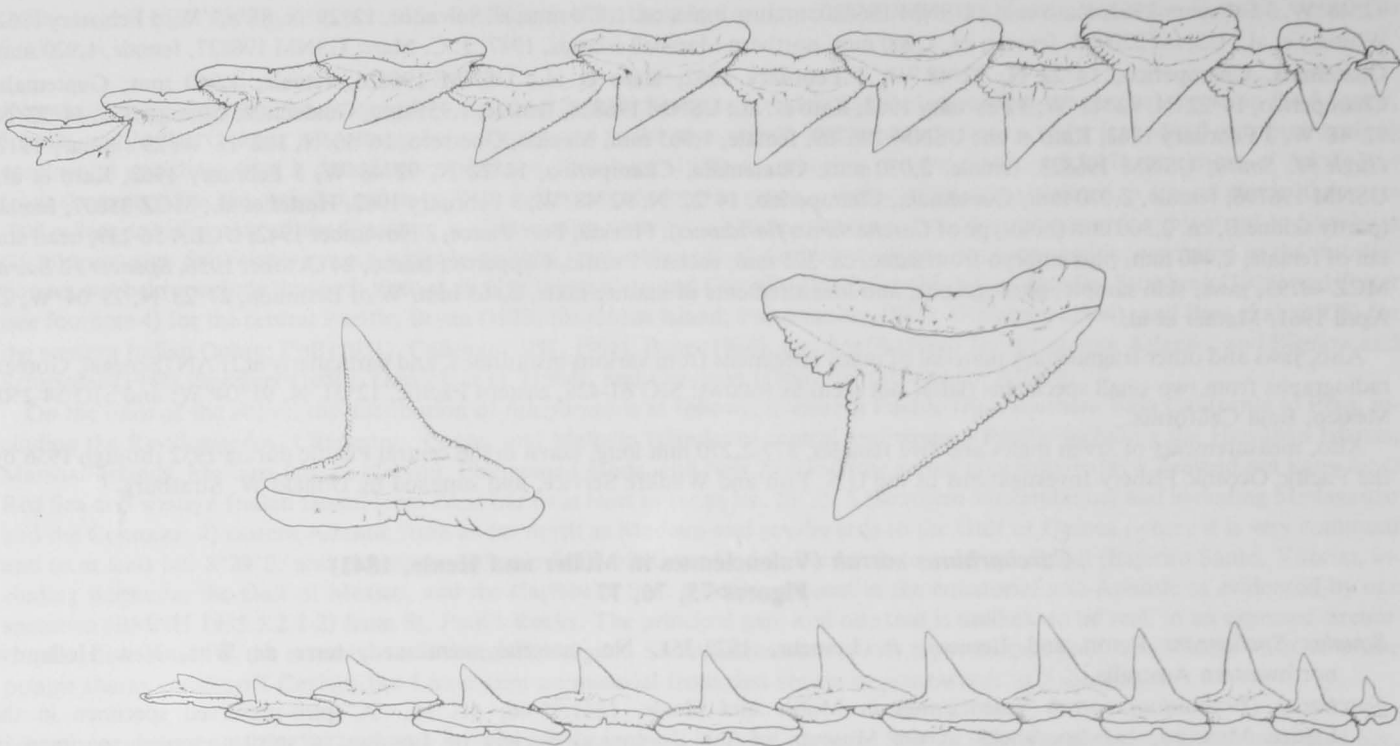


Figure 76.—*Carcharhinus sorrah*, USNM 170488, 1,160 mm TL, female from the Philippines: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

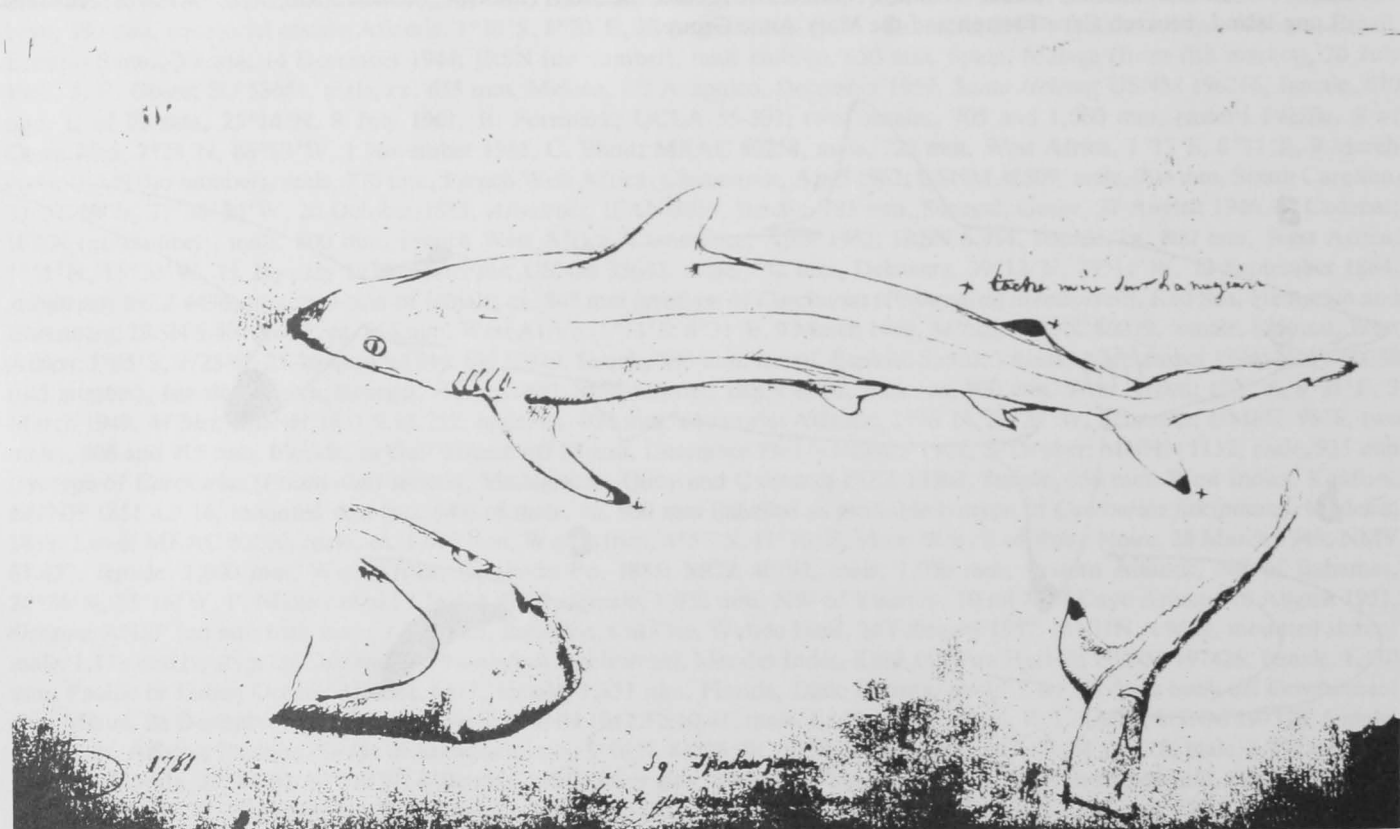


Figure 77.—Reproduction of an unpublished drawing by Lesueur labelled "*Sq. spallanzani*." The drawing and manuscripts including descriptions of *C. spallanzani* by both Peron and Lesueur are in the Museum d'Histoire Naturelle, Le Havre.

Diagnosis.—Moderate-sized sharks up to 1.55 m long, with a low, narrow interdorsal ridge; tip of pectoral, second dorsal, and lower lobe of caudal fin markedly black, but the apex of the first dorsal has only a narrow dusky to black margin; snout moderately long and pointed; internarial width 1.3–1.5 in preoral length; origin of first dorsal fin varying from slightly anterior to slightly posterior to inner pectoral corner; apex of first dorsal pointed to acute; origin of second dorsal from slightly behind origin of anal fin to about one-third back along anal base; height of second dorsal 1.5–2.2% TL and 2.0–2.6 in length of its rear tip; dental formula usually $\frac{12-1-12}{12-1-12}$ but may be $\frac{12 \text{ or } 13-1 \text{ to } 3-12 \text{ or } 13}{11 \text{ or } 12-1 \text{ or } 2-11 \text{ or } 12}$; upper teeth moderately broad, oblique, notched laterally, with noticeably coarser serrations basally; lower teeth oblique, concave to notched laterally, serrated; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 66–79; caudal centra 84–98; total centra 153–175; diplospondyly begins just behind pelvic base, from slightly in front of to slightly behind pelvic rear tip; diplospondylous centra regularly alternating in length; penultimate monospondylous centrum 0.9–1.2 times as wide as long.

This is the only ridged-backed species of *Carcharhinus* with fin tips strongly marked with black. It is similar to *falciformis* in having a very low and attenuate second dorsal fin but is easily distinguished by its color pattern, oblique lower teeth, and dental formula.

Nomenclatural discussion.—Although the name *spallanzani* Peron and Lesueur in Lesueur, 1822 is the first available name for this species, I reject it in favor of *sorrah* Valenciennes in Müller and Henle, 1841, described two decades later. My reasons for this are, firstly, that *spallanzani* cannot be identified with certainty, even to genus, from the original description and there is no type material, and secondly, despite the fact that the name *spallanzani* has had considerable usage in recent years its application has generally been incorrect.

The original description of *spallanzani* Peron and Lesueur in Lesueur (1822:351) is brief, and in total reads as follows:

“*Squalus Spallanzani*.—Peron and Lesueur.

Spiracles none; a black spot at the extremity of the pectorals, another at the summit of the second dorsal and a third at the end of the inferior lobe of the tail; caudal fin undulated above; pectorals falciform, very narrow, situate under the two last branchial openings; head very much depressed; a lunulated emargination above and another beneath the tail.

“Inhabits terre de Witt, New Holland.”

The lack of spiracles, the precaudal pits, and a caudal fin “undulated above” support its identity as a carcharhinid, but no more than that. Referral to *Carcharhinus* has depended only on the similarity between the pattern of black fin tip markings described for *spallanzani* and occurring also in several species of *Carcharhinus*, e.g., *brevipinna*, *limbatus*, and *melanopterus* as well as *sorrah*.

Difficulties in treating *spallanzani* are evident even in the early literature. Müller and Henle (1841) placed it as a synonym of the later described *melanopterus*, but without comment. Duméril (1865) tentatively assigned it to his new species *bleekeri* (= *sorrah*) and noted (footnote, p. 367) “J’aurais adopté la dénomination de *C* (Pr.) *Spallanzanii*, si la description de l’espèce australienne donnée sous ce nom par Lesueur, n’était beaucoup trop incomplète, pour qu’il soit possible de lui assigner son véritable rang.” Günther (1870) likewise considered *spallanzani* a possible synonym of *bleekeri*; Garman (1913), followed by Fowler (1941), recognized *spallanzani* as a valid species, incorporating *bleekeri* as a junior synonym. Whitley (1934, 1940, 1945) reverted to Müller and Henle’s, (1941) interpretation by making *spallanzani* a senior synonym of *melanopterus*—a surprising action in view of the fact that Whitley²⁵ had seen the same evidence used in the present study to establish *spallanzani* as synonymous with *sorrah*. More recently, Smith and Smith (1963), D’Aubrey (1964), and Bass et al. (1973) have used the name *spallanzani* in a totally different sense, by applying it to the species which I describe here as a new species, *wheeleri*.

Evidence for identifying *spallanzani* as a synonym of *sorrah* is available in manuscripts by Peron and Lesueur relating to material collected during Baudin’s expedition to “Terres australes” on the corvettes *Geographe* and *Naturaliste* in 1800–4. This expedition visited northwestern Australia (Terre de Witt) in 1801, where *spallanzani* was collected and described. I am indebted to André Maury, Directeur Conservateur of the Muséum d’Histoire Naturelle, Le Havre, who kindly provided photocopies of the relevant parts of these manuscripts from the museum archives. For *spallanzani* there are descriptions by both Peron and Lesueur, and illustrations by Lesueur.

The illustrations, reproduced here (Fig. 77), are themselves diagnostic insofar as they show a shark with a pointed snout, a very low second dorsal fin, attenuate rear tips of the first and second dorsal fins, and black tips on the pectoral, second dorsal, and lower lobe of the caudal—which in combination characterize *sorrah*. The darker of the two photocopies provided also shows, but faintly, a pencil line which could have been meant to represent an interdorsal ridge. At the bottom of the illustrations there are the words

“*Sq. spalanzani*
n’existe plus dans la Méditerranée. qq rapport avec le Glaucus.”

The manuscript descriptions are handwritten and not easy to decipher. That of Lesueur, in French, is relatively short and fairly general, but it supplements the illustrations by describing the teeth (the uppers sharp, narrow, and very wide basally where there are very fine serrae; the lowers triangular, serrated, strongly notched on the side and inclined towards the angle of the mouth) and giving the size of the specimen as 115 cm (though the 5 is questionably decipherable as such). Peron’s description is much longer, mostly in

²⁵G. P. Whitley, Honorary Associate, Australian Museum, 6–8 College St., Sydney, New South Wales, Australia, pers. commun. to J. E. Randall, Bernice P. Bishop Museum, P.O. Box 6037, Honolulu, Hawaii, December 1971.

Latin but finishing in French, and more difficult to translate. It is a general description, but there are some measurements including a total length of 109 (or 105) cm, and a brief account of the alimentary canal plus a statement that in each oviduct there were two pale yellow eggs suspended by a long brown cord (reproductive data for *sorrah* show that females may be mature at 1,100 mm and have litters of 2-6 embryos).

From the above information there can be no doubt that *spallanzani* is a senior synonym of *sorrah*. However, the only argument which could be put forward to justify the use of *spallanzani* in preference to *sorrah* would be that of priority. In all other respects (inadequate original description, lack of type material, incorrect usage) *spallanzani* has been a *nomen dubium*. Its identity could not be interpreted by normal procedures—and although the manuscript material from the Le Havre Museum now allows unequivocal interpretation, this must be regarded as fortuitous. The original authors made no mention of their fuller and supplementary manuscripts and illustrations. Accordingly, I favor the continued use of *sorrah*, though such a decision will require an appeal to the International Commission.

Of the five syntypes of *sorrah* listed in Müller and Henle, (1841:46), I have examined one in the Leiden Museum and two in the Paris Museum. The two specimens in London appear to have been lost. The spirit-preserved specimen in Leiden (RNH 4294), a female of 570 mm TL from Java, agrees with the measurements given in Müller and Henle, and according to these authors (1841:xxi) was used for their illustration in conjunction with a figure from Kuhl and Hasselt. I therefore designate this Leiden specimen as lectotype of *Car-charias* (*Prionodon*) *sorrah* Valenciennes. Of the two syntypes in the Paris Museum, one (MNHN 1131), a female of 544 mm from Pondicherry, India, is clearly *sorrah*, but the other (MNHN 1132), a male of 935 mm from Madagascar, is referable to *falciformis* as recognized here (p. 159).

Duméril (1865:367) described *bleekeri* from two Indian specimens, and indicated in a key (p. 362) that it differed from *sorrah* by having black tips on the pectorals as well as on the lower lobe of the caudal whereas *sorrah* had only the lower lobe of the caudal black tipped. Also, following his description of *sorrah* (p. 369), he noted that in *sorrah* "le museau est moins court que chez le *Pr. Bleekeri*." Bearing in mind that firstly, one of the two Paris Museum syntypes of *sorrah* which Duméril had for comparison is referable to *falciformis*, and secondly, the other syntype is a juvenile or possibly even a late embryo whereas his material of *bleekeri* included a mature male, it is understandable that he found differences. I have examined the two syntypes of *bleekeri* in the Paris Museum (mounted skins, MNHN A9584 and A9660, males of 740 and 1,280 mm, respectively, from Pondicherry) and in the light of what is now known about changes in proportions with growth I can find no reason for regarding *bleekeri* as distinct from *sorrah*.

There is no written description of *taeniatius* Hemprich and Ehrenberg (1899:8) in the account of that species, which was edited by Hilgendorf. However, the excellent illustrations of *taeniatius*, showing the elongate second dorsal fin, the black-tipped fins, the underside of the snout, and the teeth, leave no doubt that it is *sorrah*, and the locality, the Red Sea, is one where *sorrah* is known to occur. I did not find any type material of *taeniatius* in the Berlin Museum where some of Hemprich and Ehrenberg's specimens still remain, though there is one specimen there (ISZZ 10687) labelled *Prionodon taeniatius* Klunzinger, from Koseir in the Red Sea. This specimen is a male, 720 mm long, whereas the figured specimen of *taeniatius* was stated to be a female, at one-third natural size which would make it 882 mm long. Also the Berlin Museum specimen is clearly referable to the species which I describe here (p. 111) as *wheeleri*, hence could not be confused with *taeniatius* (= *sorrah*.) This specimen is possibly the one referred to by Hilgendorf in a comment under his listing of *taeniatius*.

Whitley (1947:129) in describing *isobel* from Western Australia compared it only with *fowleri* Whitley 1944 (= *ambyrhynchos* and *brevipinna*) also from Western Australia. Whitley's account and illustrations of *isobel* agree with *sorrah* in all respects. I have examined the fragmentary remains of the holotype in the Australian Museum (jaws, fins, and skin sample), and these together with entire specimens from Western Australia and Queensland confirm that *isobel* and *sorrah* are conspecific.

Description (see also Table 80).—Rather small sharks, growing to at least 1.5 m TL. Midline of back between dorsal fins with a low, narrow dermal ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles close-packed, overlapping, subcircular in outline in small specimens, rhomboid or nearly so in larger, each with three to five longitudinal ridges and a corresponding number of rather feeble posterior marginal teeth in small specimens, seven in larger.

Snout moderately long, pointed in contour. Anterior margin of eye is slightly forward of front of mouth. Nostrils strongly oblique, slitlike, the anterior margin of each with a prominent pointed lobe.

Dental formula $\frac{12-1-12}{12-1-12}$ in 8 of 15 specimens counted; $\frac{12-2 \text{ or } 3-12}{12-1 \text{ or } 2-12}$ in 4; $\frac{12-1-12}{11-1-11}$ in 2; and $\frac{13-1-12}{12-1-12}$ in 1. Upper teeth

moderately broad, oblique except for the first series on each side of symphysis, their lateral margins notched, their medial margins straight to convex, both margins serrated, the serrations moderately fine except basally where they are coarser, particularly on the lateral margins; one to three small symphyseal teeth. Lower teeth narrow, almost erect at center of mouth but increasingly oblique towards the sides, their lateral margins deeply notched, their medial margins shallowly notched to concave, both margins finely serrated; in small specimens the lateral margins have two or more large basal serrae which are themselves finely serrated but in large specimens the serrations are of uniform size; one or occasionally two small symphyseal teeth.

First dorsal fin rather low, slightly falcate in small specimens, erect in large, its apex rather sharply pointed; origin of first dorsal just anterior to or over inner (posterior) corner of pectoral fin in small specimens and subadults but slightly behind the inner pectoral corner in some larger specimens. Second dorsal fin low and long, with a noticeably attenuate rear tip, almost equal to anal fin; length of second dorsal rear tip 2.0-2.6 (mean 2.3) times second dorsal height in 11 specimens; origin of second dorsal behind anal fin origin, usually about one-third back along anal base. Pectoral fins rather short; origin of pectorals below and between the levels of the third and fourth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal fails to reach level of first dorsal axil, and reaches, variably, from halfway to four-fifths along first dorsal base.

Table 80.—*Carcharhinus sorrah*, proportional dimensions in percentage of total length.

	♂ 570 mm Java RNH 4294	♂ 584 mm China Chusan Is. SU 14247	♂ 594 mm Indian Archipelago USNM 32708	♂ 599 mm Gulf of Thailand GVF 2428	♂ 626 mm Gulf of Thailand GVF 2467	♂ 762 mm Gulf of Thailand GVF 2563	♂ 787 mm Red Sea Eritrea HU E57/665	♂ 946 mm Gulf of Thailand GVF 2563	² ♀ 1,160 mm Philippine Is. Manila Bay USNM 170488	♀ 1,266 mm Gulf of Thailand GVF 2467
Snout tip to										
outer nostrils	3.2	3.8	3.5	3.8	3.8	3.2	3.8	3.3	3.4	3.2
eye	6.5	7.5	6.8	7.4	7.2	6.8	7.8	6.6	7.3	6.7
mouth	7.1	8.3	7.6	8.3	8.0	7.3	8.4	7.1	7.7	7.2
1st gill opening	17.0	15.9	17.7	18.0	17.4	16.0	18.4	—	—	17.6
3d gill opening	19.1	18.2	20.0	20.0	19.6	18.1	21.1	—	—	19.7
5th gill opening	20.3	19.5	21.4	21.7	21.2	19.6	23.0	—	23.6	21.3
pectoral origin	19.8	18.2	20.4	20.4	20.1	18.4	22.0	19.1	—	19.7
pelvic origin	45.6	45.0	45.6	44.4	44.6	44.7	46.0	46.4	—	50.8
1st dorsal origin	28.7	28.8	28.1	28.1	28.6	27.7	31.5	28.4	—	30.8
2d dorsal origin	58.8	59.4	59.6	58.4	58.7	59.1	61.4	60.8	—	65.8
anal fin origin	57.6	58.4	57.9	57.1	57.2	57.6	60.1	60.1	—	63.6
upper caudal origin	68.8	69.9	69.6	68.4	68.8	69.3	70.8	70.1	—	74.2
lower caudal origin	68.3	69.0	69.1	68.0	68.1	68.3	70.1	69.6	—	73.8
Nostrils										
distance between inner										
corners	4.9	5.5	5.3	5.7	5.4	5.3	6.1	5.2	5.9	5.5
Mouth										
width	6.3	7.2	6.7	7.3	6.9	7.2	8.3	7.1	8.2	7.8
length	4.3	3.9	4.0	4.0	4.2	3.9	6.0	3.9	4.9	4.3
Labial furrow lengths										
upper	0.6	0.3	0.3	0.2	0.2	0.2	0.5	0.4	0.4	—
lower	0.5	0.2	0.4	0.3	0.3	0.3	0.8	0.4	0.4	—
Gill opening lengths										
1st	1.9	2.1	1.9	2.0	2.1	2.2	2.1	2.1	1.8	2.6
3d	2.5	2.6	2.1	2.7	2.6	2.8	2.6	2.8	2.2	3.3
5th	1.8	2.0	1.8	2.2	1.9	2.1	1.8	1.9	1.6	2.4
Eye										
horizontal diameter	2.3	2.4	2.2	2.3	2.2	2.0	2.0	1.7	2.0	1.7
1st dorsal fin										
length of base	8.6	9.0	9.9	9.3	8.8	8.9	9.7	9.4	10.4	10.2
length posterior margin	3.9	3.4	4.0	3.3	4.0	4.0	3.7	3.5	4.1	3.9
height	7.8	8.0	7.7	8.2	8.1	8.8	9.2	8.5	9.1	9.7
2d dorsal fin										
length of base	2.9	3.3	3.0	3.0	3.0	2.9	3.2	2.7	3.3	2.6
length posterior margin	4.0	3.6	4.1	3.9	4.2	3.8	3.8	3.9	4.3	4.5
height	1.6	1.7	1.9	1.5	1.7	1.6	1.8	1.7	2.2	1.9
Anal fin										
length of base	4.0	4.0	4.7	4.7	4.3	4.7	4.5	3.8	3.7	4.3
length posterior margin	3.9	3.8	3.9	3.7	4.1	3.9	4.2	4.0	4.6	4.3
height	2.5	2.8	2.2	2.4	2.8	2.6	2.7	2.8	3.0	2.8
Pectoral fin										
length of base	5.2	5.7	5.1	5.5	5.7	5.6	5.8	6.0	6.9	5.6
length anterior margin	14.6	14.7	15.7	14.5	15.6	16.3	15.8	15.5	17.1	15.8
length distal margin	10.2	10.8	10.4	11.0	10.7	11.9	11.3	11.3	14.0	13.6
greatest width	6.8	—	—	7.7	7.8	8.0	8.4	7.4	—	8.1
Pelvic fin										
length of base	4.6	4.5	4.7	4.7	4.8	4.3	5.5	5.1	5.8	4.7
length anterior margin	4.7	4.6	4.5	4.5	4.6	4.7	5.0	4.4	5.6	4.7
length distal margin	4.4	3.9	4.2	4.2	4.1	4.2	4.7	4.5	4.9	4.9
length of claspers	—	2.2	2.2	2.2	2.0	2.5	2.9	2.3	—	—
Caudal fin										
length of upper lobe	31.2	30.7	30.6	31.7	31.2	31.1	29.4	30.2	27.6	27.0
length of lower lobe	11.8	11.7	11.3	10.7	11.6	12.5	12.1	11.8	12.2	11.9
Trunk at pectoral origin										
width	8.8	11.1	—	9.5	10.0	9.8	12.7	9.7	—	11.0
height	8.9	11.3	—	10.3	10.8	10.2	8.7	10.8	—	13.4
Dental formula	12-1-12	12-1-12	12-1-12	12-1-12	12-3-12	12-1-12	12-1-12	12-2-12	12-1-12	—
Vertebrae	12-1-12	12-1-12	11-1-11	12-1-12	12-1-12	12-1-12	12-1-12	12-1-12	12-2-12	—
precaudal	66	68	67	66	68	67	73			
caudal	87	86	86	93	92	90	93			
total	153	154	153	159	160	157	166			

¹Syntype of *Carcharias (Prionodon) sorrah*.²Dimensions from a skinned out specimen, hence some measurements are of doubtful value.

Color in life was very fully described by Fourmanoir (1961:36) as follows: "La région dorso-latérale est gris rosé, le bord de la 1^{re} dorsale est entouré de noir, la 2^e dorsale a son sommet noir, coloration pouvant s'étendre vers la base et vers l'arrière, son prolongement postérieur est généralement noir sur une longueur variable. Les pectorales, qui sont noires d'une façon régulière au sommet sur la face interne, présentent une zone de noir terminale, variable, sur la face externe qui est de couleur dominante grise. Le sommet externe des pelviennes est quelquefois noir (fig. 27). La caudale est soulignée de noir, à l'exception du bord ventral du lobe inférieur; le lobe inférieur est en général noir dans la partie distale, la coloration pouvant s'étendre jusqu'à l'échancrure. La pupille est large et noire."

After preservation in alcohol the general body color is gray or brownish gray above, pale to yellowish or white below; ventral lobe of caudal prominently black tipped; apex of second dorsal fin black, and often the posterior half of the rear tip black also, these two black areas usually separated by a gray or pale area along the anterior half of the rear tip; pectoral tip dusky to black; first dorsal fin with a small dusky region at the apex and with narrow dusky margins; upper and terminal margins of dorsal lobe of caudal fin with narrow dusky margins.

Vertebral counts of seven specimens are given in Table 80 and of another 14 specimens in Table 81. Examination of the precaudal counts on a regional basis shows that specimens from the western Indian Ocean and Red Sea have higher counts (73-79) than those from the western Pacific and Indo-Australian region (66-71).

Centrum diameter greater than centrum length except in the last five or six monospondylous centra which are about square or even longer than wide. Diplospondyly begins behind the pelvic base, usually above the posterior tip of the pelvic fin but slightly anterior or posterior to that level in some specimens. Diplospondylous centra regularly alternating in length, the shorter centrum of each pair varying from two-thirds to three-fourths as long as the longer adjacent centrum. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was the 0.84-1.07 (mean 0.98) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.42-1.78 (mean 1.59) in 13 specimens.

The smallest apparently free-living specimen (but still with an umbilical scar not fully healed, and hence possibly a late embryo) that I have seen was 544 mm TL, while the largest embryo was 450 mm. Males examined by me have been predominantly juvenile, and in seven immature specimens up to 964 mm long the clasper length was from 2.0 to 2.9% TL. One larger male of 1,280 mm was obviously mature judging by clasper length, though the latter was not measured. Fourmanoir (1961) reported that in his Madagascar material maturity was reached at 1,600 mm, but he did not state whether this applied to males, and in any case this size is rather too large for minimum size at maturity in either sex judging by other data available. Gohar and Mazhar (1964) noted that in their Red Sea specimens a male of 1,135 mm was mature, and Bass et al. (1973) recorded six mature males from the southwestern Indian Ocean with lengths ranging from 1,060 to 1,250 mm. Wheeler (1953, as *menisorrah*) reported a mature male of 1,240 mm from the Mauritius-Seychelles area. For females, Bass et al. (1973) found that maturity was reached at 1,100-1,160 mm. The smallest mature females listed by other authors were 1,320 mm (Wheeler 1953, as *menisorrah*) and 1,365 mm (Gohar and Mazhar 1964). The few available data on the number of embryos per litter and embryo size, etc. are as in Table 82.

Table 81.—Vertebral numbers in 14 specimens of *Carcharhinus sorrah*.

Specimens	Precaudal	Caudal	Total
GVF 1512 Gulf of Thailand	69	85	154
GVF 2465 Gulf of Thailand	66	89	155
GVF 1557 Gulf of Thailand	66	87	153
MNHN 1131 India, Pondicherry ¹	71	93	164
WAM P.6173 Western Australia	71	84	155
USNM 198167 Madagascar	76	98	174
3 specimens, Mozambique Channel ²	74-76	—	170
5 specimens, St. Brandon ²	76-79	—	170-175
Range (including counts from Table 80)	66-79	84-98	153-175

¹Syntype of *Carcharias (Prionodon) sorrah*.

²Counts from Bass et al. (1973).

Table 82.—Number of embryos per litter and size of embryos in *Carcharhinus sorrah*.

Total length of female (mm)	No. of embryos	Total length of embryos (mm)	Month	Locality	Source
1,320	2	—	September	Mauritius-Seychelles area	Wheeler (1953, as <i>menisorrah</i>)
1,365	5	230-250	December	Red Sea	Gohar and Mazhar (1964)
1,380	2	—	July	Mauritius-Seychelles	Wheeler (1953, as <i>menisorrah</i>)
1,440	6	320-380	March	Red Sea	Gohar and Mazhar (1964)
—	3	—	—	Southwestern Indian Ocean	Bass et al. (1973)
—	—	360-380	October	Southwestern Indian Ocean	Bass et al. (1973)
—	—	500	November	Southwestern Indian Ocean	Bass et al. (1973)

Bass et al. (1973) estimated that the "... young are probably dropped during the summer," and that size at birth is from 500 to 600 mm. Fourmanoir (1961), who had observed a free-living specimen of 600 mm, with the umbilical scar not healed, taken in January, suggested that it was born in December at a length of about 570 mm. The largest specimens examined by me were a female of 1,266 mm and a male of 1,280 mm, but these are less than maximum size, particularly for females which have been reported as reaching 1,380 mm (Bass et al. 1973), 1,440 mm (Gohar and Mazhar 1964), 1,500 mm (Wheeler 1953, as *menisorrah*), and 1,550 mm (Fourmanoir 1961). The data given above on size at maturity suggest that maximum size would be considerably less than 2 m TL, and hence cast doubt on the identification of two females of 1,980 and 2,300 mm which Fourmanoir (1961) recorded from Madagascar.

Distribution (see also Material examined).—Specimens of *sorrah* that I have examined confirm that this species has an essentially tropical distribution centered on the Indian Ocean, and extending from the Red Sea and western Indian Ocean eastwards to the Indo-Australian region and the western Pacific to as far as China, the Philippines, and Australia. It does not appear to be present in Oceania. My data cover localities in the Red Sea, Gulf of Aden, west coast of Madagascar, Seychelles, Mauritius, India (Pondicherry), China (Chusan Island and Canton), Hong Kong, Gulf of Thailand, Philippines (San Roque and Manila Bay), Singapore, Borneo, Java, and Australia (Western Australia at Exmouth Gulf and at about lat. 21°S, and Queensland).

Literature listings of *sorrah* from other localities, which although not confirmable from the accounts are very likely to be correct, include Malaya, Sumatra, the Solomons, and Bombay and various other Indian localities. Bass et al. (1973) reviewed the literature records for the western Indian Ocean and showed that although *sorrah* is present from the Red Sea to as far south as lat. 24°55'S (Mozambique Channel) there are "As yet only two specimens... recorded from the African coast...."

Reports of *sorrah* from Oceania stem from Günther (1910) who recorded the species from the Hawaiian Islands, and from Fowler (1928, 1938) who listed it from the Hawaiian Islands and the Marquesas, but both these authors' accounts depend on recognizing *Carcharias phorcys* Jordan and Evermann 1904 as a synonym of *sorrah*. As shown elsewhere in this account (p. 31) *phorcys* is referable to *limbatus* and, as I have no other evidence to suggest that *sorrah* occurs in Oceania, Günther's and Fowler's listings cannot be substantiated.

Material examined.—WAM P. 6173, embryo, 325 mm, Western Australia, Exmouth Gulf, October 1958, R. McKay; BMNH (uncat.), male embryo, 330 mm, Borneo, W. Frank; NMV 61-383, embryo, 385 mm, Canton, Raybough; SMF 763, two embryos, male, 390 mm, and female, 403 mm, Red Sea, 1828, Rüppell; BMNH 1925.7.20.1-6, six embryos, four females, 390-450 mm, and two males, 420 and 430 mm, Gulf of Aden, A. Ehrenreich; ISZZ 14575, female embryo, 425 mm, Singapore, G. Schneider; MNHN 1131, female, 544 mm [syntype of *Carcharias (Prionodon) sorrah*], India, Pondicherry, Bélanger; GVF 1512, female, 544 mm, Gulf of Thailand, Aangtong Bay off Goh Samui, 9°30'55"N, 99°55'15"E, 6-8 November 1957; NMV 61-386, female, 545 mm, Red Sea, Djibuti, 1905; GVF 2469, female, 557 mm, Gulf of Thailand, about 50 mi offshore E of Prachuap Khiri Khan Town, ca. 11°40'-11°51'N, 100°34'-100°39'E, 10-16 January 1961; RNH 4294, female, 570 mm [syntype of *Carcharias (Prionodon) sorrah*], Java; GVF 1557, male, 575 mm, Gulf of Thailand, near Sriracha Village, 13°09'-13°13'N, 100°52'-100°55'E, 9-10 December 1957; BMNH 1939.3.23.2, female, 578 mm, Hong Kong, Herklots; SU 14247, male, 584 mm, China, Chusan Island, Tinghai, 16 October 1936, A. W. Herre; NMV 61-421, male, 590 mm, Mauritius, 1888; USNM 32708, male, 594 mm, Indian Archipelago; GVF 2428, male, 599 mm, Gulf of Thailand, Chon Buri Province, 27 September 1960; BMNH 81.10.20.94, male, 605 mm, Museum Godeffroy; NMV 61-359, female, 607 mm, Borneo, 1897; GVF 2467, male, 626 mm, and female, 1,266 mm, Gulf of Thailand, Trat Province, about 2 to 3 mi offshore W and WSW of Goh Chang, ca. 11°56'-12°03'N, 102°14'30"-102°17'45"E, 12 January 1960; USNM 198167, male, 638 mm, Madagascar, Nossi Bé, 30 April 1964, R. F. Cressy; USNM 170558, female, 738 mm, Philippine Islands (via San Roque Market), 1 December 1908, *Albatross*; MNHN A 9584, mounted skin of male, ca. 740 mm [syntype of *Carcharias (Prionodon) bleekeri*], India, Pondicherry, Leschenault; GVF 2563, four males, 762-980 mm, and female, 822 mm, Gulf of Thailand, Surat Thani Province, about 5 mi offshore E of Goh Samui, ca. 9°32'15"N, 100°09'45"E, 6-8 May 1961; HU E 57/665, male, 787 mm, Red Sea, Eritrea, October-December 1957, A. Ben Tuvia; QMB I. 6885, male, 812 mm, Queensland, Salamander Rocks, February 1940, G. Coates; ISZZ 10688, male, 830 mm, Red Sea, Koseir, Klunzinger; NMV 61-452, two females, 835 and 1,005 mm, Red Sea, 1896; AMS IB.1493, jaws, dorsal and anal fins, and skin sample of female, 910 mm [holotype of *Galeolamna (Galeolamnoides) isobel*], Western Australia, Long Island between Cape Preston and the Mary Anne Group; NMV 61-438, two females, 1,038 and 1,165 mm, Red Sea, Hamfila, 1896; USNM 170488, female, 1,160 mm, Philippine Islands, Manila Bay, La Monja Island, 7 February 1909, *Albatross*; MNHN A9660, mounted skin of mature male, 1,280 mm [syntype of *Carcharias (Prionodon) bleekeri*], India, Pondicherry, Leschenault; BMNH 67.8.16.78, head and fins of mature male, Seychelles, Playfair; SMNS 2745, jaws, Red Sea, Koseir, 1879, Klunzinger.

Carcharhinus brachyurus (Günther, 1870) Figures 78, 79, 80, 81

Carcharias brachyurus Günther, 1870:369. Four specimens listed under description, viz "a. Stuffed, 7 3/4 feet [2,362 mm] long. Antarctic Expedition. b. Stuffed, 44 inches [1,118 mm] long. New Zealand. Presented by Sir J. Ross. c, d. Foetus. Australia."

Carcharias lamiella Jordan and Gilbert, 1883b:110-111. Holotype, young male specimen, 2 ft (610 mm) long, San Diego Bay, Calif.; also jaws of an adult example from Lower California.

Eulamia ahenea Stead, 1938:98-105. Measurements given of three male specimens, 105 in (2,667 mm), 98 in (2,489 mm), and 100½ in (2,553 mm) TL, from off Sydney, N.S.W., Australia; description based on third-mentioned specimen; holotype (heart and teeth in half of jaws) in Australian Museum presumably from one of above.

Carcharinus improvisus Smith, 1952a:760-765, text fig. 1. Holotype, female, 635 mm, South Africa, Algoa Bay.

Carcharhinus rochensis Abella, 1972:102-106, figures. Holotype, adult male, Uruguay, Rocha; two paratypes, adult male and juvenile male, Uruguay, Rocha.

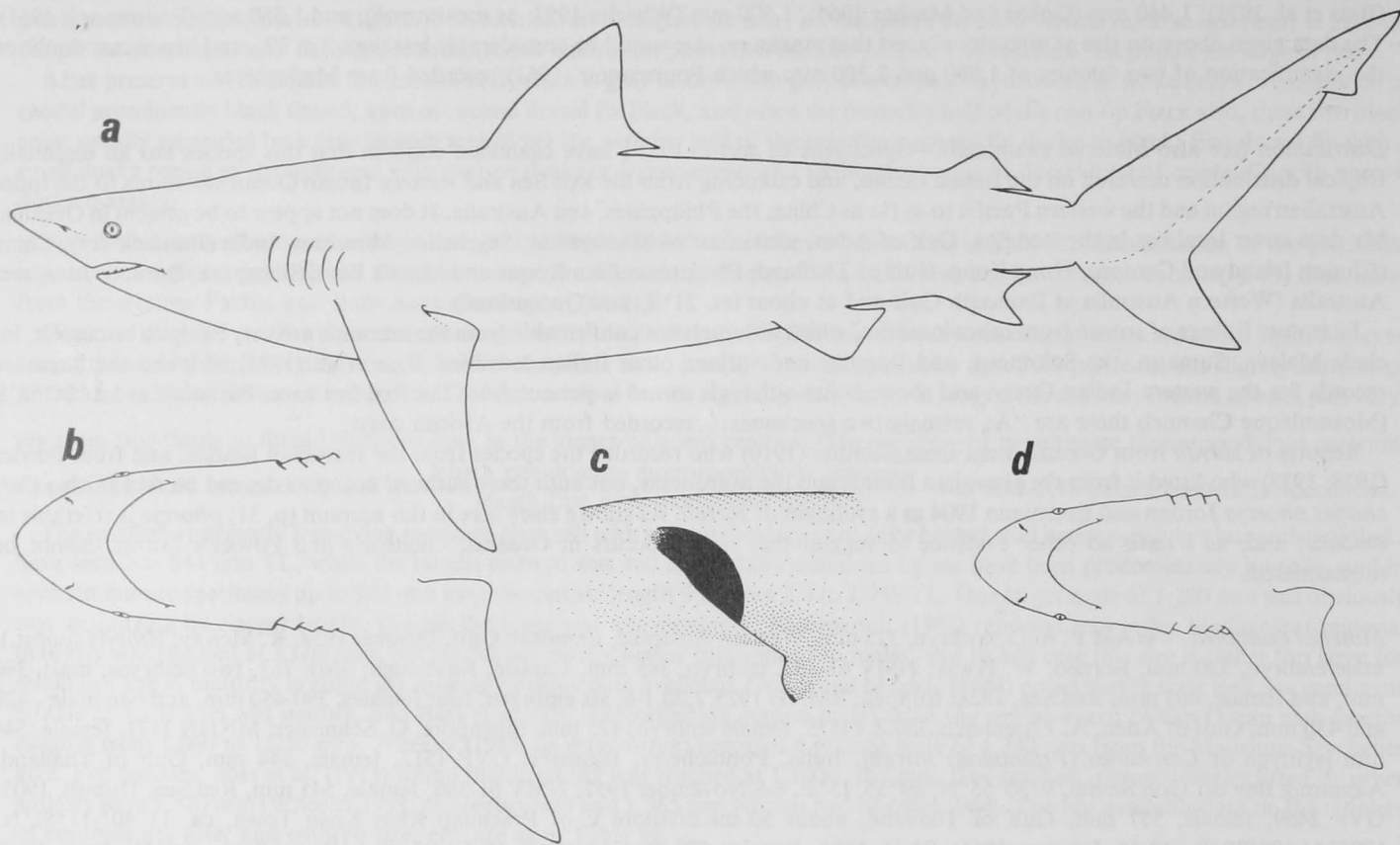


Figure 78.—*Carcharhinus brachyurus*, DM 2262, neotype, 2,420 mm TL, female from New Zealand: *a*, left side; *b*, underside of head; *c*, enlarged left nostril; *d*, underside of head of UCLA 59-300, 2,348 mm TL, male from California.

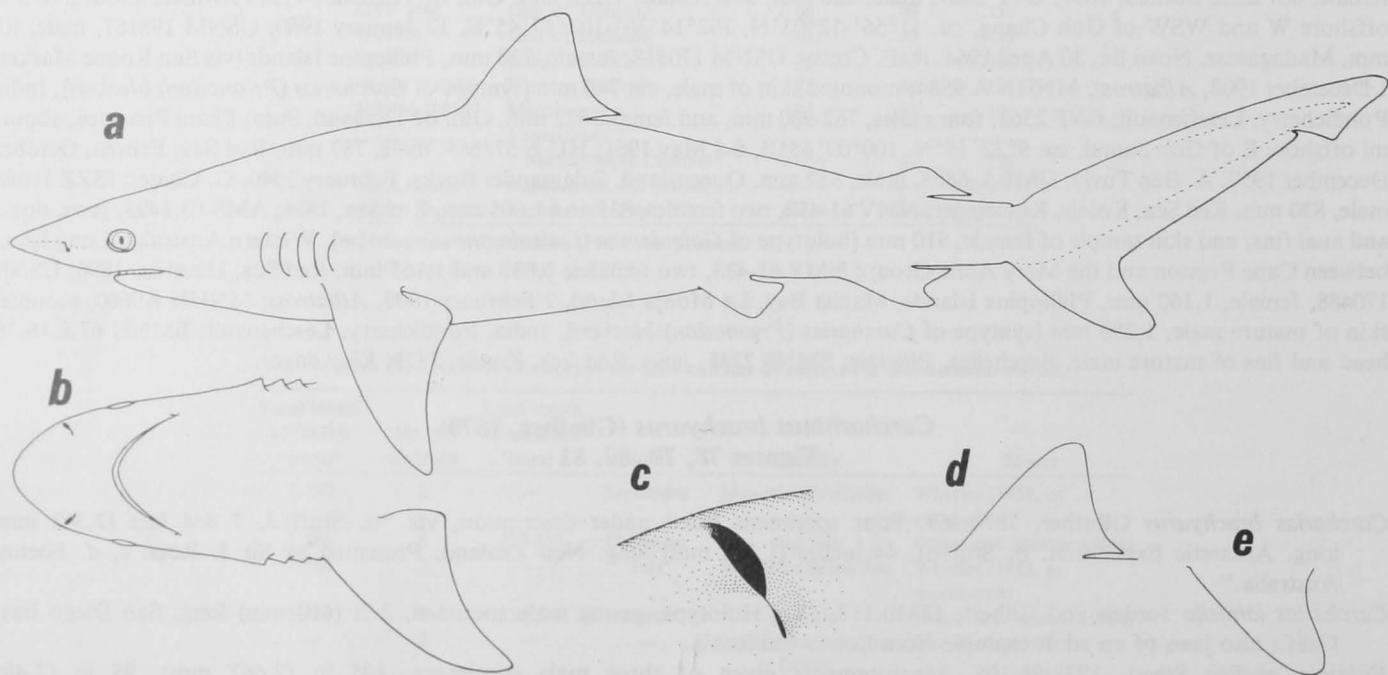


Figure 79.—*Carcharhinus brachyurus*, DM 3025, 719 mm TL, male from New Zealand: *a*, left side; *b*, underside of head; *c*, enlarged left nostril; *d*, first dorsal fin of SI0 60-380, 737 mm TL, female from Mexico, Baja California; *e*, lower caudal lobe of same.

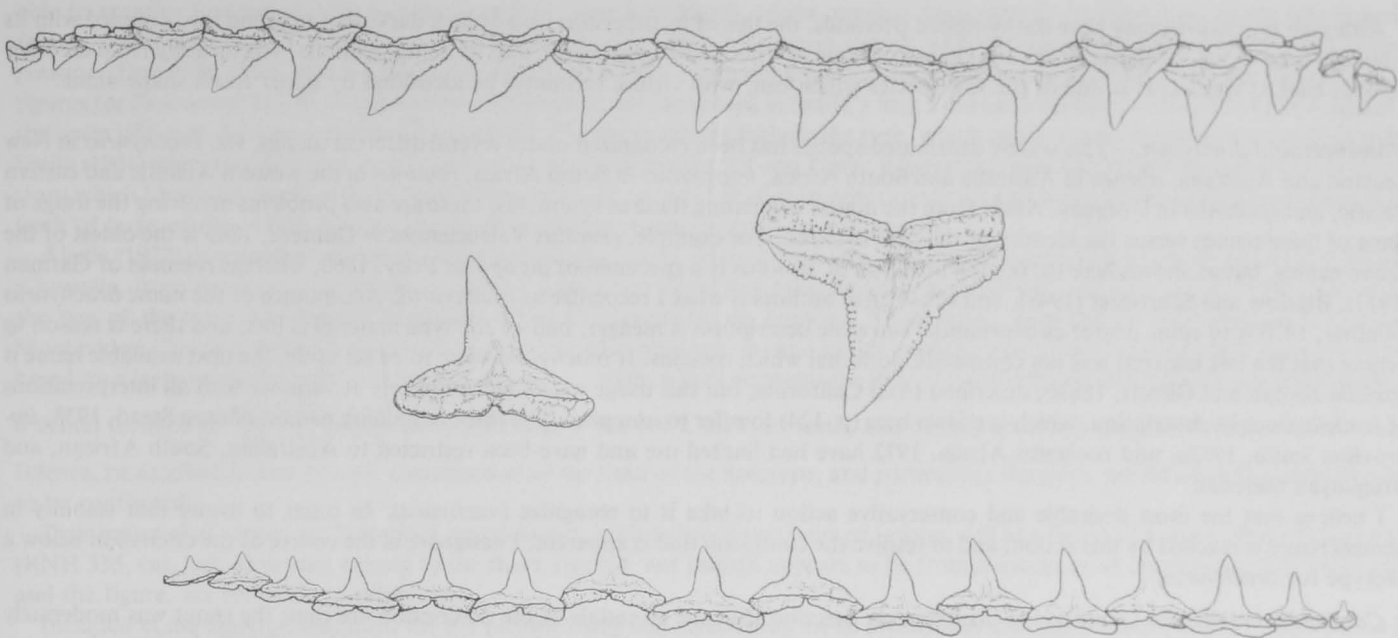


Figure 80.—*Carcharhinus brachyurus*, USNM 197663, 2,900 mm TL, female from South Africa, Algoa Bay: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

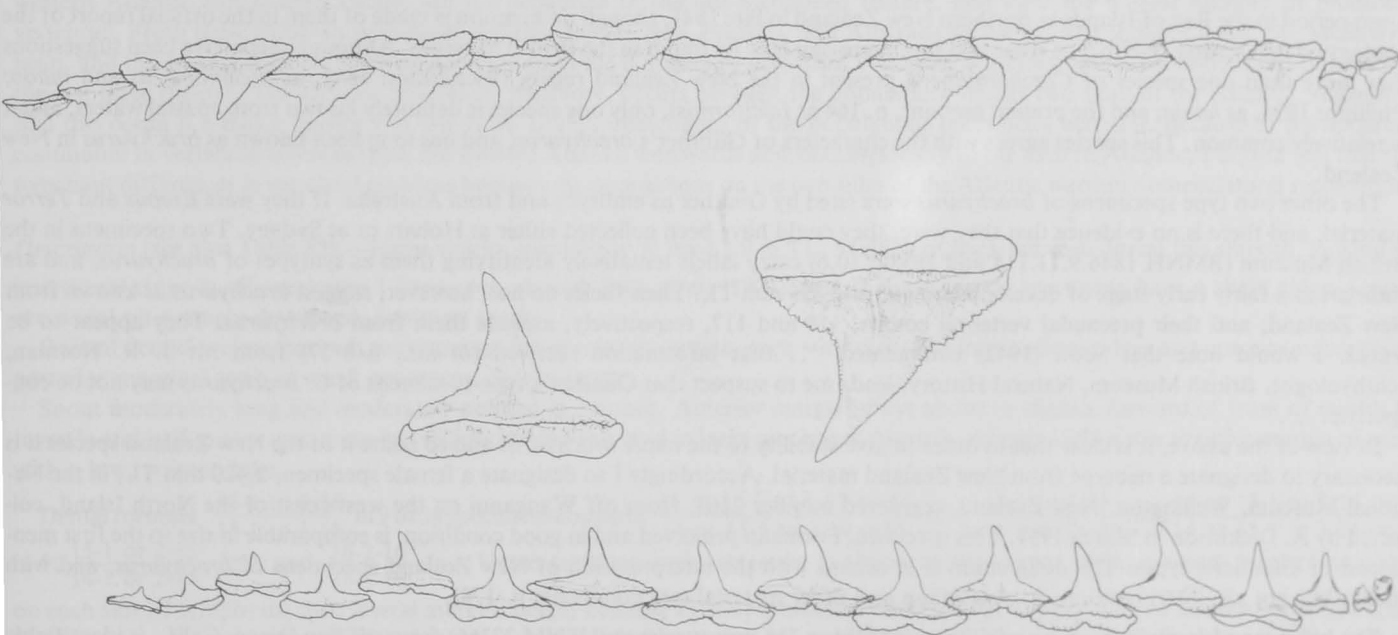


Figure 81.—*Carcharhinus brachyurus*, SAMC 23071, mature male from Cape Town: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and lower teeth.

Diagnosis.—Large sharks, up to 2.92 m long, usually lacking an interdorsal ridge; tips of some fins, particularly the pectorals, and leading margins of dorsals and upper lobe of caudal fin frequently dusky to blackish, more so in juveniles than adults; snout of moderate length and sharply rounded to pointed; internarial width 1.1-1.4 in preoral length; origin of first dorsal fin over or slightly anterior to inner pectoral corner; apex of first dorsal somewhat rounded to pointed; origin of second dorsal fin about over or usually slightly behind anal fin origin; height of second dorsal 1.9-2.6% TL and 1.2-1.8 in length of its rear tip; dental formula usually $\frac{15 \text{ or } 16-2-15 \text{ or } 16}{15-1-15}$ but may be $\frac{14 \text{ to } 16-1 \text{ to } 3-14 \text{ to } 16}{14 \text{ or } 15-1 \text{ to } 3-14 \text{ or } 15}$; upper teeth moderately narrow, oblique, deeply concave to notched laterally, weakly concave to notched medially, with slightly coarser serrations basally; lower teeth erect to slightly oblique, serrated; teeth of adult males narrower, more oblique or curved and with finer serrations than those of adult females; no obvious discrete series of enlarged hyomandibular pores alongside corner of mouth; precaudal centra 96-110; caudal centra 86-94; total centra 179-203; diplospondyly begins from origin to middle of pelvic base; diplospondylous centra regular in length; penultimate monospondylous centrum 1.2-1.5 times wider than long.

Although *brachyurus* may have dusky-tipped pectorals, the tips of its other fins usually lack dark markings and this, coupled with its relatively long snout, its characteristically shaped oblique or "hooked" upper teeth, and its dental formula, sets it aside from all other smooth-backed species. It is one of the few species which can, with virtual certainty, be identified by upper tooth shape alone.

Nomenclatural discussion.—This widely distributed species has been recognized under several different names, viz. *brachyurus* in New Zealand and Australia, *ahenea* in Australia and South Africa, *improvisus* in South Africa, *remotus* in the western Atlantic and eastern Pacific, and *rochensis* in Uruguay. Apart from the matter of relating these as synonyms, there are also problems involving the usage of some of these names versus the identity of the type material. For example, *remotus* Valenciennes in Duméril, 1865 is the oldest of the above names, but as shown here (p. 66) the holotype of *remotus* is a specimen of *acronotus* Poey, 1860, whereas *remotus* of Garman (1913), Bigelow and Schroeder (1948), and subsequent authors is what I recognize as *brachyurus*. Acceptance of the name *brachyurus* Günther, 1870 is to some degree circumstantial since the description is meager, half of the type material is lost, and there is reason to believe that the lost material was not conspecific with that which remains. If *brachyurus* were to be set aside, the next available name is *lamiella* Jordan and Gilbert, 1883b, described from California, but this usage would be completely at variance with all interpretations of *lamiella* since its description, which is shown here (p. 124) to refer to *obscurus*. The three remaining names, *ahenea* Stead, 1938, *improvisus* Smith, 1952a, and *rochensis* Abella, 1972 have had limited use and have been restricted to Australian, South African, and Uruguayan material.

I believe that the most desirable and conservative action to take is to recognize *brachyurus*. In order to assure that stability in nomenclature is reached by this action, and to resolve the confusion that is apparent, I designate in the course of the discussion below a neotype for *brachyurus*.

Carcharias brachyurus Günther was inadequately described but the essentials of the description are that: the snout was moderately long and rather pointed; the teeth in both jaws were serrated; the upper teeth were oblique and notched laterally, the lower teeth narrow and erect; the second dorsal fin and the anal fin were opposite each other; the coloration was uniform; and New Zealand was the type locality. Of the four type specimens listed under the description, the first two were mounted skins, one about 2,360 mm from "Antarctic Expedition," the other of about 1,110 mm from New Zealand and presented by J. Ross. Presumably these two specimens were collected in the course of the voyage of the *Erebus* and *Terror* to Antarctica in 1839-43, commanded by James Ross, which included a 3-mo period in the Bay of Islands in northern New Zealand in late 1841, though no mention is made of them in the official report of the zoology of that voyage. Neither of these two specimens can now be found in the British Museum. Although there have been suggestions that more than one species of *Carcharhinus* is present in the New Zealand region (Richardson 1843, as *melanopterus* and *maoo*; Philipps 1924, as *lamia*; and the present account, p. 164 as *falciformis*), only one species is definitely known from coastal waters, and it is relatively common. This species agrees with the characters of Günther's *brachyurus*, and has long been known as *brachyurus* in New Zealand.

The other two type specimens of *brachyurus* were cited by Günther as embryos and from Australia. If they were *Erebus* and *Terror* material, and there is no evidence that they were, they could have been collected either at Hobart or at Sydney. Two specimens in the British Museum (BMNH 1846.9.11.118 and 1953.5.10.6) carry labels tentatively identifying them as syntypes of *brachyurus*, and are embryos at a fairly early stage of development, 496 and 305 mm TL. Their facies do not, however, suggest *brachyurus* as known from New Zealand, and their precaudal vertebral counts, 118 and 117, respectively, exclude them from *brachyurus*. They appear to be *leucas*. I would note that Scott (1942) commented "...that information received (*in litt.*, 6/8/37) from Mr J. R. Norman, Ichthyologist, British Museum, Natural History, leads me to suspect that Günther's type-specimens of *C. brachyurus* may not be conspecific. . . ."

In view of the above, it is clear that in order to give stability to the name *brachyurus* and to relate it to the New Zealand species it is necessary to designate a neotype from New Zealand material. Accordingly I so designate a female specimen, 2,420 mm TL, in the National Museum, Wellington, New Zealand, registered number 2262, from off Wanganui on the west coast of the North Island, collected by A. Dickinson in March 1957. This specimen, Formalin preserved and in good condition, is comparable in size to the first mentioned of Günther's types. The designation is in accord with the interpretation of New Zealand specimens of *brachyurus*, and with many, but not all, interpretations of Australian and other material (see comments p. 178).

The holotype of *lamiella* Jordan and Gilbert (1883b), a 718 mm specimen (USNM 27366) from off San Diego, Calif., is identifiable as *brachyurus*, but subsequent interpretations of *lamiella* can be referred to *obscurus* (see p. 124). It is possible that the latter species was what Jordan and Gilbert had in mind when they described *lamiella*, for this would explain their description of the snout as "...wide and rounded" and their comment that a (paratype) "...pair of jaws taken from a much larger specimen have, as usual, the teeth considerably broader than in the young and more distinctly serrate"—these are features which do not fit *brachyurus* but are applicable to *obscurus*. The paratype jaws have not been located. The inference from these discrepancies in the description is that Jordan and Gilbert saw adult material (of *obscurus*) and wished to describe it as *lamiella*, but in selecting a small specimen as holotype (a common practice of many ichthyologists faced with the problems of preserving, transporting, and curating museum specimens of such large fishes as sharks) they inadvertently obtained a juvenile of *brachyurus*.

Stead's (1938) description of *ahenea* from Sydney was based on three adult males. Type material comprises only a heart and one-half of the upper and lower jaws, presumably from one of the three males though there is nothing to indicate which one. The description of *ahenea*, and the jaws of the type with their characteristically shaped upper teeth, leave no doubt that *ahenea* and *brachyurus* are conspecific. Stead regarded *ahenea* as distinct from other Australian whaler sharks, including *brachyurus*, in its bronze color. His discussion covering likely synonyms of *brachyurus* shows that he identified as *brachyurus* a species which enters estuaries and rivers, and which can, with confidence, be referred to *leucas*.

Smith's (1952a) account of *improvisus*, based on a single female specimen, 635 mm long, from Algoa Bay, South Africa, is not separable from *brachyurus* when variation from a range of material is taken into account. Through the courtesy of E. Johnson I was

able to examine a series of fresh specimens at Port Elizabeth, South Africa, ranging from embryos to very large adults (the largest a female, 2,900 mm). Smith regarded *improvisus* as a species which "... agrees exactly with the description and figures of *Carcharinus remotus* (Duméril), 1865, as given by Bigelow and Schroeder..." except for some slight differences in proportions which he listed (the figures for first dorsal height of *improvisus* and *remotus* are transposed in Smith's list). I did not find these differences to be constant in the series of South African specimens I examined. The latter did not include the type, which could not be found at Rhodes University. Smith (1961) later identified as *ahenea* a large male specimen taken off Cape Town; it is evident from this identification and from discussions which I had with Smith that he was not aware of the extent of change in proportions with growth and of sexual dimorphism in the teeth of large adults, which provide the basis for synonymizing *improvisus* and *ahenea*.

Abella (1972) described *rochensis* from three male specimens, whose lengths were not stated except that two were adults and one was a juvenile, from the coast near Rocha, Uruguay. I have not found any other account of *rochensis*, and have been unable to ascertain the size of the types which were deposited in the Departamento de Zoología Vertebrados, Facultad de Humanidades y Ciencias, Montevideo. The fact that only the heads of the types (plus photographs and measurements) were preserved suggests that *rochensis* was based on a large or moderately large species. The description, which mentions the lack of an interdorsal ridge, no obvious fin markings, a dental formula of $\frac{15-2-15}{15-1-15}$, and the illustrations of the shark itself, its teeth, and dermal denticles, can, with a high degree of confidence, be ascribed to *brachyurus*. Examination of the head of the holotype, and particularly the teeth, would allow this identification to be confirmed.

Type material of *japonicus* Temminck and Schlegel, 1850 included two pairs of jaws as well as a figure of a shark. One of these pairs (RNH 335, cat. ost. a) cannot belong to the shark figured, but instead appears to be from a specimen of *brachyurus*. The other pair, and the figure, are referable to *plumbeus*.

Included in the material examined for the present study and referred by me to *brachyurus* is a pair of jaws (WAM P. 6667) cited by Whitley (1944) as additional material to his type series of *Galeolamna* (*Galeolamnoides*) *eblis* from Western Australia. The remainder of the type material of *eblis* is identifiable as *obscurus* (see p. 122).

I have not found any consistent differences in body proportions, shapes of fins, etc., or teeth in material from different and widespread localities, but there is circumglobal clinal variation in the number of precaudal vertebrae (see p. 177). Specimens from the western Atlantic and eastern Pacific are not separable in the last-mentioned feature, and have the highest number of precaudal vertebrae. From these localities westwards through Japan, New Zealand, and Australia to the western Indian Ocean, the Mediterranean, and the eastern Atlantic there is a diminution in the numbers of precaudal vertebrae, with the lowest and comparable numbers in the last three regions. The greatest difference, therefore, occurs between the populations on the two sides of the Atlantic, suggesting that this ocean is a major barrier and that little, if any, interchange of the populations takes place across it. Because of the apparent continuum in vertebral numbers from the western Atlantic westwards and circumglobally to the eastern Atlantic, I do not feel that the trenchant differences in vertebral numbers between the populations on the two sides of the Atlantic warrant nomenclatural recognition.

Description (see also Table 83).—Large sharks, growing to at least 2.9 m TL. Midline of back between dorsal fins smooth, lacking an interdorsal ridge in all specimens I have seen, though Bass et al. (1973) note that occasional specimens have a slight ridge. Upper precaudal pit strongly developed, lower pit weak.

Dermal denticles close-packed, overlapping, subcircular in outline, each with three low longitudinal ridges and corresponding short posterior marginal teeth in small specimens, five in larger.

Snout moderately long and moderately pointed in contour. Anterior margin of eye above or slightly forward of front of mouth in juvenile and half-grown specimens but slightly behind this level in large specimens. Nostrils oblique, slitlike, the anterior margin of each with a low, pointed lobe.

Dental formula $\frac{16-1 \text{ to } 3-16}{15-1 \text{ to } 3-15}$ in 9 of 34 specimens counted; $\frac{15 \text{ or } 16-1 \text{ to } 3-15 \text{ or } 16}{14 \text{ or } 15-1 \text{ to } 3-14 \text{ or } 15}$ in 9; $\frac{15-1 \text{ to } 3-15}{15-1 \text{ or } 2-15}$ in 8; $\frac{14 \text{ or } 15-1 \text{ to } 3-14 \text{ or } 15}{14 \text{ or } 15-1 \text{ to } 3-14 \text{ or } 15}$ in 5; $\frac{15-1 \text{ or } 2-15}{14-1 \text{ or } 2-14}$ in 2; and $\frac{16-2-16}{15-1-16}$ in 1. Upper teeth narrowly triangular to almost scythe-shaped, oblique except for the first series on each side of symphysis, their lateral margins deeply concave to almost notched, their medial margins convex distally but with a concavity or even a notch nearer to the base, both margins finely serrated, the serrations somewhat irregular and coarser basally; one to three small symphyseal teeth. Lower teeth narrow, erect or only slightly oblique, both margins concave to notched basally but the medial margins slightly to moderately convex distally, very finely serrated; one to three small symphyseal teeth. The teeth of large, mature adults are sexually dimorphic—those of males being proportionately longer and narrower, more oblique to curved laterally, and with finer serrations than in females. Such dimorphism has so far been noted in specimens from the eastern Atlantic, from South Africa, and from New Zealand.

First dorsal fin moderately low, its apex erect and rather blunt in small specimens but slightly falcate and more pointed in adults; origin of first dorsal over or sometimes just anterior to inner (posterior) corner of pectoral fin. Second dorsal fin moderately high and long, distinctly smaller than anal fin; length of second dorsal rear tip 1.2-1.8 (mean 1.4) times second dorsal height in 18 specimens; origin of second dorsal above or more often slightly behind anal fin origin, usually above the anterior one-fourth of anal base. Pectoral fins moderately long and slender; origin of pectorals below the level of the fourth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches almost or quite to level of first dorsal axil in small specimens, and to as far back as halfway along first dorsal rear tip in larger.

Color in life of Australian specimens was described by Stead (1938, as *ahenea*) as "When fresh a bronze-brass colour 'like a new penny', almost pale golden at times; grey or cream strip along sides from eyes; creamy white below." Sadowsky (1967b), describing Brazilian specimens, noted that "Fresh specimens are olive-gray above, paler below, the fins with very slightly darker edges. After a few hours the back assumes a bronze color." After preservation in alcohol the color is gray or brownish gray above, paler below, usually

Table 83.—*Carcharhinus brachyurus*, proportional dimensions in percentage of total length.

	♂ 660 mm Japan near Niigata UMMZ 177120	♀ 688 mm Brazil Rio de Janeiro MCZ 703	♂ 718 mm California San Diego Bay USNM 27366	719 mm New Zealand Awanui DM 3025	♀ 752 mm N.W. Africa Rio de Oro IRSN 6913	♂ 840 mm Peru Guanape Cove UCLA 58-112	♀ 1,230 mm "Constanti- nopol near Trieste" NMV —	♀ 1,257 mm South Africa Algoa Bay —	♀ 2,420 mm New Zealand Wanganui DM 2262	♀ 2,725 mm South Africa Algoa Bay USNM 197671
Snout tip to										
outer nostrils	3.8	3.9	3.8	3.6	4.2	4.2	4.1	4.1	3.3	3.4
eye	7.7	7.4	7.2	7.0	8.2	8.1	7.7	7.4	7.0	5.9
mouth	7.7	7.0	7.1	7.2	8.4	7.9	7.7	7.5	6.4	5.7
1st gill opening	19.1	18.3	18.2	18.2	19.8	19.8	—	18.9	18.6	17.1
3d gill opening	—	20.7	20.5	20.9	22.6	—	—	21.8	21.7	19.5
5th gill opening	23.3	22.5	22.5	23.2	24.3	23.9	—	23.6	24.4	21.5
pectoral origin	21.8	21.9	21.7	23.0	23.3	23.1	25.2	23.0	23.8	20.2
pelvic origin	50.6	49.6	49.0	49.9	50.2	50.6	53.3	51.7	55.2	52.5
1st dorsal origin	32.6	32.0	31.5	31.7	34.0	32.5	33.9	32.3	33.7	31.2
2d dorsal origin	63.5	63.2	62.1	62.3	63.0	64.3	64.8	65.0	67.3	64.9
anal fin origin	62.3	61.7	62.3	59.9	62.1	64.0	63.9	64.3	67.3	64.7
upper caudal origin	74.3	73.6	72.4	72.7	73.2	74.1	74.7	74.7	76.2	75.2
lower caudal origin	73.0	72.0	71.4	72.2	72.2	73.6	73.7	73.7	76.4	74.0
Nostrils										
distance between inner corners	5.6	5.3	5.6	5.8	6.5	5.6	5.9	5.9	6.0	5.3
Mouth										
width	6.7	7.3	7.7	8.8	8.6	7.7	8.5	8.4	8.7	7.8
length	4.5	5.2	4.7	4.6	5.2	4.8	4.5	4.5	4.5	4.0
Labial furrow lengths										
upper	0.5	0.6	0.6	0.7	0.8	0.4	0.4	0.6	0.7	0.5
lower	—	0.3	0.5	—	0.7	0.4	0.3	0.5	0.3	0.4
Gill opening lengths										
1st	—	2.6	2.4	3.1	2.6	2.7	2.9	3.1	3.5	2.9
3d	2.5	2.9	3.1	3.5	3.2	3.0	3.7	3.5	4.1	3.6
5th	—	2.5	2.2	2.5	2.6	2.0	2.4	2.5	2.7	2.3
Eye										
horizontal diameter	2.1	2.0	1.8	2.1	2.2	1.9	1.7	1.7	1.1	1.1
1st dorsal fin										
length of base	8.9	9.3	9.8	10.1	9.8	9.9	9.2	10.4	10.1	10.8
length posterior margin	2.7	2.8	2.8	2.8	2.8	2.7	3.0	2.8	3.2	2.4
height	6.8	7.8	8.1	8.2	8.5	8.3	9.0	8.5	9.7	8.9
2d dorsal fin										
length of base	3.6	3.1	3.8	4.3	4.1	3.7	3.9	3.6	3.9	3.5
length posterior margin	3.0	3.2	3.6	3.1	3.4	3.1	3.2	3.2	3.1	2.9
height	2.1	2.2	2.2	2.2	2.5	2.0	2.3	2.5	2.5	2.3
Anal fin										
length of base	4.8	4.1	3.6	5.4	4.2	3.8	4.4	4.1	4.5	4.0
length posterior margin	2.6	2.8	3.3	2.9	3.1	3.0	3.1	2.9	2.8	2.7
height	3.2	3.1	3.1	2.9	3.5	3.1	3.0	3.5	3.7	3.7
Pectoral fin										
length of base	5.9	5.8	6.1	6.1	6.0	5.4	6.0	6.5	6.4	6.8
length anterior margin	16.7	17.7	17.0	16.0	18.1	18.0	18.2	18.3	21.3	19.2
length distal margin	12.0	13.6	12.8	12.1	14.3	14.3	14.0	14.9	18.0	15.1
greatest width	8.6	8.7	9.1	9.6	9.2	9.5	8.9	9.5	10.7	9.6
Pelvic fin										
length of base	5.2	4.9	5.0	4.2	5.3	5.2	5.1	5.0	6.2	5.0
length anterior margin	5.0	5.4	5.2	5.0	5.3	5.5	5.2	5.6	6.0	5.1
length distal margin	5.3	5.1	5.4	4.7	5.8	5.2	5.5	5.9	6.0	5.9
length of claspers	1.5	—	2.1	2.2	—	2.4	—	—	—	—
Caudal fin										
length of upper lobe	26.7	27.3	27.4	27.8	26.8	27.9	26.2	25.8	27.5	25.3
length of lower lobe	10.4	12.0	12.2	12.2	11.3	12.4	11.5	11.6	13.4	12.1
Trunk at pectoral origin										
width	11.0	10.3	11.7	12.5	11.3	11.2	12.2	12.1	13.2	13.2
height	10.0	9.5	9.7	13.5	11.0	—	11.4	11.0	13.6	—
Dental formula	15-2-15 14-2-14	—	15-2-16 14-1-14	16-1-16 15-1-15	15-1-15 14-1-14	16-1-16 15-1-15	14-2-15 14-1-14	15-2-15 15-1-15	15-2-15 15-2-15	15-2-15 15-1-15
Vertebrae										
precaudal	108	—	110	104	99	—	—	99	—	98
caudal	93	—	91	93	92	—	—	89	—	—
total	201	—	201	197	191	—	—	187	—	—

¹Holotype of *Carcharias lamiella*.²Neotype of *Carcharhinus brachyurus*.

with a horizontal band of the paler color extending along the midlevel of each side from the pelvic region forward to below the first dorsal base, but this is not always evident on adults; small specimens have a dusky color on the underside of the pectoral fin tips, and dusky leading margins on the first and second dorsal fins and upper lobe of the caudal fin; in adult specimens these dusky markings are less pronounced though usually there is dusky on the underside of the pectoral tips.

Vertebral counts of six specimens are given in Table 83 and these are repeated in Table 84 together with counts of another 22 specimens arranged by locality on a circumglobal basis to show that western Atlantic and eastern Pacific specimens have the highest (and comparable) precaudal counts, while specimens from west of these localities have fewer precaudal centra, the lowest precaudal counts occurring in the western Indian Ocean, the Mediterranean, and the eastern Atlantic. Bass et al. (1973) reported that 41 specimens from South Africa had precaudal counts of 96-103, with a mean of 99.5. Their total counts for 37 specimens were 179-193 (mean 185.9).

Centrum diameter considerably greater than centrum length even in longest monospondylous centra at posterior of abdomen. Diplospondylous centrum length regular. Diplospondyly begins above anterior to middle of pelvic base. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.67-0.82 (mean 0.75) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.14-1.39 (mean 1.26) in 12 specimens.

Table 84.—Vertebral numbers in 28 specimens of *Carcharhinus brachyurus*.

Specimens		Precaudal	Caudal	Total
MCZ 703	Brazil	109	89	198
MCZ 703	Brazil	108	89	197
USNM 27366	California ¹	110	91	201
SIO 50-200	California	109	88	197
SIO 60-380	California	108	91	199
SIO (uncat.)	California	109	94	203
SIO 65-681	California	109	—	—
USNM 127775	Peru	110	90	200
USNM 127775	Peru	110	92	202
UMMZ 117120	Japan	108	93	201
IRSN 1355	Japan	106	85 +	191 +
DM 3025	New Zealand	104	93	197
USNM 28666	Australia	104	89	193
BMNH 1922.13.2	S. Africa, Algoa Bay	98	89	187
USNM 197622	S. Africa	98	86	184
	S. Africa, Algoa Bay ²	99	89	188
	S. Africa, Algoa Bay ²	99	90	189
	S. Africa, Algoa Bay ²	100	—	—
	S. Africa, Algoa Bay ²	99	—	—
	S. Africa, Algoa Bay ²	99	—	—
	S. Africa, Algoa Bay ²	99	—	—
	S. Africa, Algoa Bay ²	98	—	—
	S. Africa, Algoa Bay ²	98	—	—
	S. Africa, Algoa Bay ²	98	—	—
	S. Africa, Algoa Bay ²	96	—	—
NMV 39352				
(old number)	Mediterranean, Nice	100	89 +	189 +
MNH 98-1229	Mediterranean, Nice	99	88 +	187 +
IRSN 6913	Northwest Africa	99	92	191
Range		96-110	86-94	184-203

¹Holotype of *Carcharias lamiella*.

²One of 10 freshly caught specimens, 1,230-2,900 mm long, kindly made available at Port Elizabeth in May 1963 by E. Johnson; precaudal counts made by dissection, and specimens later discarded.

The smallest, apparently free-living specimen I have seen was 585 mm TL, while the largest embryo was 670 mm. The smallest mature male measured by me was 2,348 mm long, with a clasper length of 8.4% TL. Sadowsky (1967b) reported (as *remotus*) that five mature males from Brazil, 2,414-2,549 mm long, had clasper lengths ranging from 6.4% to 8.4% TL. Stead (1938), in describing *ahenea* from Australia, recorded clasper lengths of 12.4 and 10.2% in two males of 2,545 and 2,580 mm, respectively, but I do not know the manner in which he made his clasper measurements. The smallest mature male found by Bass et al. (1973) in their extensive range of South African material was 2,120 mm long. Of the three gravid females that I have examined, one, 2,490 mm long from California, contained 7 embryos about 560 mm long in late July while 2 others, 2,725 and 2,900 mm long from Algoa Bay, South Africa, in early May, contained 18 embryos (610-670 mm) and 22 embryos (460-500 mm). Bass et al. (1973) recorded six pregnant females, 2,470-2,920 mm long, from South Africa; the number of embryos ranged from 13 to 20, with a mean of 16; no seasonality was apparent from their data. A litter of 23 embryos was reported by Hildebrand (1946) from a female taken in late March at Punta Coles, Peru; Hildebrand identified the species as *aethalorus* but I have seen two of the embryos (USNM 127775, 505 and 518 mm) which are definitely *brachyurus*. The small number of embryos in the Californian specimen mentioned above compared with the large numbers in the South African and Peruvian specimens is notable, and further investigation of this feature is warranted. Size at birth was estimated by Bass et al. (1973) to

be 600-700 mm, which is in agreement with my data. Their largest embryos were 590-630 mm, and their smallest free-living specimen was 720 mm. The largest male *brachyurus* clearly identifiable as such that I have seen or has been reported in the literature is a mounted specimen about 2,700 mm long, in the South African Museum. Bass et al. (1973) reported a comparable-sized male of 2,660 mm also from South Africa. However, Scott (1942) has provisionally identified as *brachyurus* a male, 2,835 mm long, taken in the River Tamar, Tasmania, and now represented by a mounted skin in the Queen Victoria Museum, Launceston, Tasmania; the overall facies of this specimen, including the teeth, as illustrated in Scott agree with *brachyurus* but the second dorsal fin is shown as larger than the anal fin—this may have been distorted in mounting, or it may be incorrectly drawn. The largest female *brachyurus* examined by me was one of 2,900 mm TL, from Algoa Bay, South Africa; Bass et al (1973) recorded another South African one of similar size (2,920 mm).

Distribution (see also Material examined).—Based on specimens I have seen, *brachyurus* is a worldwide coastal species principally in the subtropical-warm-temperate belts but with some records from tropical latitudes. Its known and rather patchy distribution from my material, plus a few other published records which are clearly *brachyurus*, is as follows: western South Atlantic from southern Brazil [Rio de Janeiro, and also Cananéia from Sadowsky's (1967b) account as *remotus*], Uruguay, and from northern Argentina [Buenos Aires from Lahille's (1928) account as *lamia*]; eastern Atlantic from northwest Africa (Rio de Oro), "tropical Atlantic," and from the southwest coast of South Africa; Mediterranean from Nice and from "Constantinopel near Trieste" (the latter enigmatic locality from a specimen in the Vienna Museum); western Indian Ocean from Durban (D'Aubrey 1964, as *ahenea*) where it is occasionally taken, and southwards to the tip of South Africa where it is common (Bass et al. 1973); eastern Indian Ocean and western Pacific from Australia (Esperance and Coventry Reef in Western Australia, off Sydney in New South Wales, and from Tasmania, if Scott's 1942 identification can be verified), New Zealand (particularly the North Island and Cook Strait), and Japan (Tokyo and Niigata); and eastern Pacific from southern California, Baja California, and from Peru (Punta Coles, Payta, and Guanape Cove).

The apparent absence of *brachyurus* from the western North Atlantic is surprising in view of the widespread distribution of this species in other oceans, and its presence in the western South Atlantic, the tropical eastern North Atlantic, and the Mediterranean. Its occurrence in the Mediterranean has not previously been noted.

Waite's (1921) listing of *brachyurus* from South Australia includes a very good illustration of the species. Two literature records definitely not applying to *brachyurus* are an earlier record of Waite (1906) from Australia whose material in this account is referable to *leucas*, and one of Schultz (1953) from the Marshall Islands whose specimens were *longimanus*.

Material examined.—IRSN 1335, two female embryos, 350 and 367 mm, Japan, Tokyo, Scheinder; NMV 61-396 and 61-387, four embryos, two males, 380 and 460 mm, and two females, 450 and 460 mm, Japan, Tokyo, 1885, Steindachner; MNHN 98-1229, two embryos, female, 400 mm, and male, 410 mm, France, Nice, Moreau; NMV 61-413, female embryo, ca. 420 mm, France, Nice, 1889; MNHN 98-1227, male embryo, 420 mm, France, Nice, Moreau; ISZZ 12248, female embryo, 430 mm, Japan, Tokyo, Doderlein; USNM 197663, three embryos, female, 475 mm, and two males, 490 and 500 mm, and jaws of mother, 2,900 mm, South Africa, Algoa Bay, 2 May 1963, E. Johnson; NMV 39352 (old number), male embryo, 465 mm, France, Nice, 1881, Steindachner; USNM 127775, two female embryos, 505 and 518 mm, Peru, Punta Coles, M. J. Lobell; USNM 28666, female embryo, 525 mm, Australia, north of Mt. Maclay, Australian Museum; NMV 61-351, male embryo, 545 mm, Australia, Sydney, Australian Museum; MCZ 703, two males, 585 and 683 mm, and female, 688 mm, Brazil, Rio de Janeiro, Thayer Expedition; NMV (no number), female, 600 mm, 1874, Steindachner; USNM 197663, three embryos, two females, 620 and 670 mm, and male, 620 mm, and jaws of mother, 2,725 mm, South Africa, Algoa Bay, 2 May 1963, E. Johnson; UMMZ 177120, male, 660 mm, Sea of Japan near Niigata Market, 18-20 August 1929, C. L. Hubbs and K. Sakamoto; USNM 197672, female, 666 mm, South Africa, Algoa Bay, 2 May 1963, E. Johnson; MCZ 693, male, 672 mm, Peru, Payta, Hassler Expedition; DIRU, two females, 702 and 847 mm, South Africa, Algoa Bay; USNM 27366, male, 718 mm (holotype of *Carcharias lamiella*), California, San Diego Bay, D. S. Jordan and C. H. Gilbert; DM 3025, male, 719 mm, New Zealand, Awanui, 28 February 1955, F. Begley; SIO 50-200, male, 730 mm, California, San Diego County, N of Oceanside, 22 July 1950, R. Kane; SIO 60-380, female, 737 mm, Mexico, Baja California, Bahia Sebastian Vizcaino, 15 September 1960; IRSN 6913, female, 752 mm, northwest Africa, Rio de Oro, Pulpito Bay, 25 November 1936, *Mercator*; BMNH 1922.1.13.2, female, 765 mm, South Africa, Natal, Knysna, Marley; NMV 39364 (old number), female, 800 mm, France, Nice, 1898, Steindachner; UCLA 58-112, male, 840 mm, Peru, Guanape Cove, 8°26'S, 78°57'W, 29 November 1957; SIO (no number), male, 850 mm, California, San Diego County, off Oceanside; WAM P.6667, jaws of female, 935 mm [additional material to type series of *Galeolamna (Galeolamnoides) eblis*], Western Australia, Coventry Reef, W. B. Alexander; NMV (no number), female, 1,230 mm, Constantinopel near Trieste [sic], 1 November 1906; — two females, 1,257 and 1,697 mm, and four males, 1,300-1700 mm, examined and later discarded except for the jaws of two (USNM 197664, 197665), South Africa, Algoa Bay, 2 May 1963, E. Johnson; UCLA 59-300, mature male, 2,348 mm, California, Los Angeles County, 6 mi SE of San Pedro Light, 13 May 1959; DM 2262, female, 2,420 mm (neotype of *Carcharias brachyurus* as designated here), New Zealand, Wanganui, March 1957, A. Dickinson; SIO 65-681, female, 2,490 mm, California, San Diego County, 21 July 1965, L. Saraspe; SAMC (no number), mounted skin of mature male, ca. 2,700 mm, South Africa, Cape Town.

Also jaws and fragments as follows: AMS IB.501, partial jaws and heart of large adult (holotype of *Eulamia ahenea*) Australia, off Sydney; DM, jaws of six specimens from New Zealand localities including Awanui, Wanganui Beach, Te Horo, Wellington Harbour, and Cape Palliser; IFAN, jaws of two adults, one male, one female, the female labelled "tropical Atlantic," 9 September 1962, *Seiju Maru*; DIRU, jaws of three specimens, one labelled Algoa Bay, West Bird Island; RNH 335, cat. ost. a, jaws of one specimen [syntype of *Carcharias (Prionodon) japonicus*], Japan, D. W. Burger; AMS IB.1618, jaws and skin fragments of female, Western Australia, Rossiter Bay, Esperance, 25 January 1944; SAMC 23071, jaws of mature male, South Africa, Cape Town, False Bay, 1961. Also jaws of three adults from New Zealand, two of them (male, 2,185 mm, female, 2,590 mm) from off Hawke Bay, loaned by F. Robson, the other, male 2,600 mm, from off Great Barrier Island, loaned by crew member of *W. J. Scott*.

Carcharhinus borneensis (Bleeker, 1858-59)

Figures 82, 83

Carcharias (*Prionodon*) *borneensis* Bleeker, 1858-1859:8-10. Male, 249 mm, from sea at Singkawang, Borneo.

Diagnosis.—Small sharks, probably not exceeding 1.00 m long, lacking an interdorsal ridge; tip of first dorsal fin dark brown to dusky, and a narrow dusky margin on upper lobe of caudal; snout long and pointed; internarial width 1.3-1.5 in preoral length; origin of first dorsal fin slightly anterior to inner pectoral corner; apex of first dorsal bluntly pointed; origin of second dorsal above or slightly behind middle of anal base; height of second dorsal 1.8-2.0% TL and 2.2-2.4 in length of its rear tip; dental formula usually $\frac{12-1-12}{11-1-11}$ but may be $\frac{11 \text{ or } 12-1-11 \text{ or } 12}{11 \text{ or } 12-0 \text{ or } 1-11 \text{ or } 12}$ upper teeth moderately narrow, oblique, deeply notched laterally, uniformly serrated except for bases

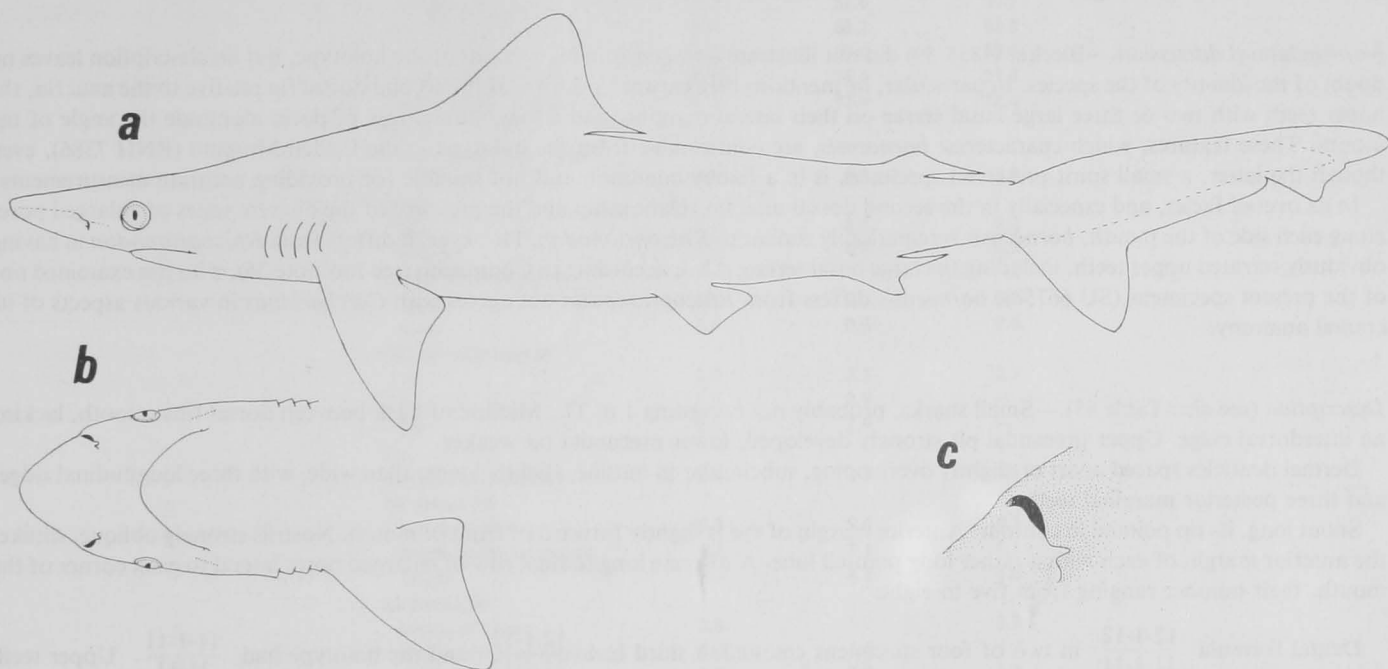


Figure 82.—*Carcharhinus borneensis*, SU 66750, 466 mm TL, female from China, Chusan Island: a, left side; b, underside of head; c, enlarged left nostril.

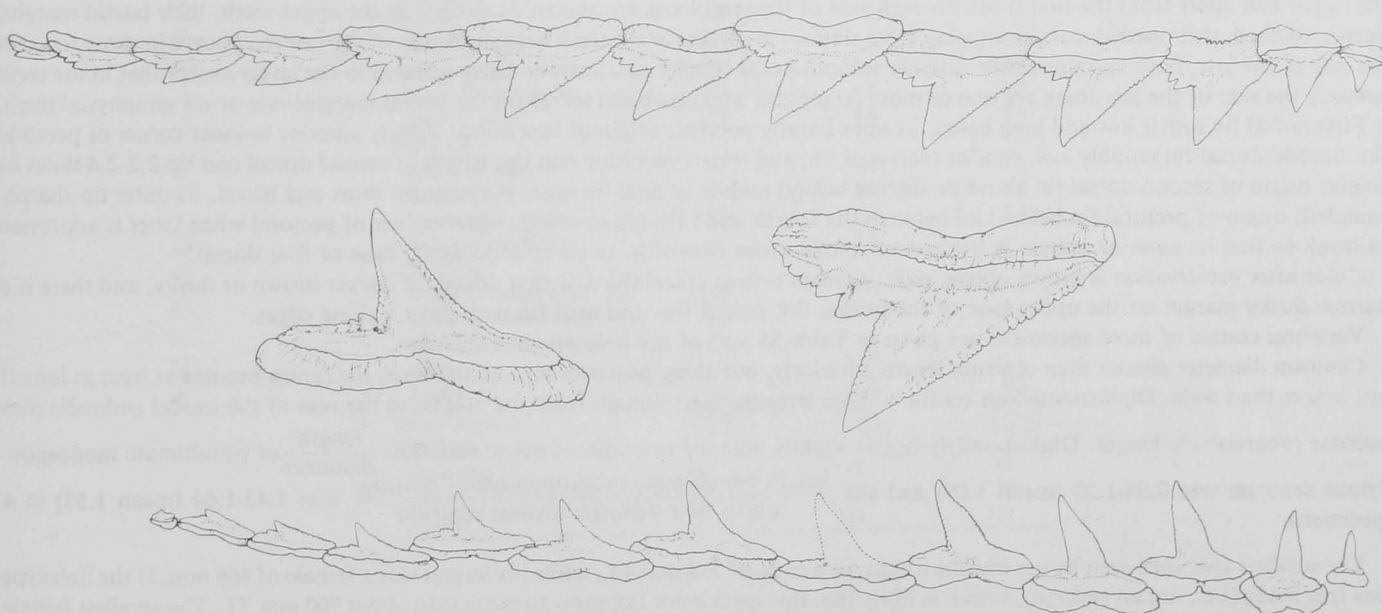


Figure 83.—*Carcharhinus borneensis*, SU 66750, 466 mm TL, female from China, Chusan Island: right upper and lower teeth (symphysis to the right); inset teeth are enlarged fifth upper and sixth lower teeth.

of lateral margins which carry two or three very large serrae; lower teeth oblique, notched laterally, smooth to serrated; an obvious discrete series of five to eight enlarged hyomandibular pores alongside each corner of mouth; precaudal centra 61-63; caudal centra 56-58; total centra 118-121; diplospondyly begins slightly in front of pelvic origin; diplospondylous centra regular in length except that they become progressively longer towards end of caudal peduncle; penultimate monospondylous centrum 0.8-1.1 times as wide as long.

This species differs from all other species of *Carcharhinus*, but agrees with *Rhizoprionodon* in possessing an obvious, discrete row of enlarged hyomandibular pores alongside each corner of the mouth. It is also similar to *Rhizoprionodon* in having the second dorsal fin origin over or slightly behind the middle of the anal base. Features which separate it from *Rhizoprionodon* include its obviously serrated teeth, the enlarged basally situated serrae on the lateral margins of the upper teeth (and to a lesser extent on the lower teeth), and its much shorter lower labial furrows (not more than 0.6% TL and not visible when mouth is closed whereas in *Rhizoprionodon* they are never less than 1.0% TL and always visible). Also, according to Compagno²⁶ who has examined one of the present specimens of *borneensis* (SU 66750), it differs from *Rhizoprionodon* but agrees with *Carcharhinus* in various aspects of its cranial anatomy. Compared with all other species of *Carcharhinus* it is unique in having the transition from monospondyly to diplospondyly occurring slightly in front of the pelvic origin rather than above or behind the pelvic base.

Nomenclatural discussion.—Bleeker (1858-59) did not illustrate *borneensis* in his account of the holotype, but his description leaves no doubt of the identity of the species. In particular, he mentions the rearward position of the second dorsal fin relative to the anal fin, the upper teeth with two or three large basal serrae on their lateral margins, and a longitudinal row of pores alongside the angle of the mouth. These features, which characterize *borneensis*, are confirmable from the holotype in the Leiden Museum (RNH 7386), even though the latter, a small spirit-preserved specimen, is in a flabby condition and not suitable for providing accurate measurements.

In its overall facies, and especially in the second dorsal-anal fin relationship and the presence of the discrete series of enlarged pores along each side of the mouth, *borneensis* is remarkably similar to *Rhizoprionodon*. However, it differs from *Rhizoprionodon* in having obviously serrated upper teeth, including the large basal serrae. Also, according to Compagno (see footnote 26), who has examined one of the present specimens (SU 66750), *borneensis* differs from *Rhizoprionodon* but agrees with *Carcharhinus* in various aspects of its cranial anatomy.

Description (see also Table 85).—Small sharks, probably not exceeding 1 m TL. Midline of back between dorsal fins smooth, lacking an interdorsal ridge. Upper precaudal pit strongly developed, lower precaudal pit weaker.

Dermal denticles spaced apart or slightly overlapping, subcircular in outline, slightly longer than wide, with three longitudinal ridges and three posterior marginal teeth.

Snout long, its tip pointed in contour. Anterior margin of eye is slightly forward of front of mouth. Nostrils strongly oblique, slitlike, the anterior margin of each with a rather long pointed lobe. A discrete longitudinal row of enlarged pores lateral to each corner of the mouth, their number ranging from five to eight.

Dental formula $\frac{12-1-12}{11-1-11}$ in two of four specimens counted; a third had $\frac{12-1-12}{11-1-12}$ and the holotype had $\frac{11-1-11}{11-11}$. Upper teeth rather narrow and oblique except for the first tooth on each side of the symphysis, their lateral margins deeply notched, their medial margins almost straight, both margins finely serrated except for the lower parts of the lateral margins which from notch to base mostly have two or three very large serrae which may themselves carry fine serrations; one small symphyseal tooth. Lower teeth narrower than the upper and apart from the first tooth on each side of the symphysis are almost as oblique as the upper teeth, their lateral margins deeply notched, their medial margins ranging from sinuous in outline in the teeth near the center of the jaw to concave in those towards the side of the jaw, both margins either virtually smooth in the smaller specimen or finely serrated in the larger except that in the teeth towards the side of the jaw there are one or more larger and irregular basal serrae on the lateral margin; one or no symphyseal teeth.

First dorsal fin rather low and long based, its apex bluntly pointed; origin of first dorsal slightly anterior to inner corner of pectoral fin. Second dorsal fin notably low, smaller than anal fin, and with a very long rear tip; length of second dorsal rear tip 2.2-2.4 times its height; origin of second dorsal fin above or slightly behind middle of anal fin base. Pectoral fin short and broad, its outer tip sharply rounded; origin of pectoral fin below and between the fourth and fifth gill openings; outer corner of pectoral when latter is adpressed to trunk so that its anterior margin is horizontal reaches from two-fifths to three-fifths along base of first dorsal.

Color after preservation is brown above, pale to cream below; apical third of first dorsal fin darker brown or dusky, and there is a narrow dusky margin on the upper lobe of the caudal fin; paired fins and anal fin with paler trailing edges.

Vertebral counts of three specimens are given in Table 85 and of the holotype in Table 86.

Centrum diameter greater than centrum length anteriorly, but along posterior half of abdomen the centra become at least as long if not longer than wide. Diplospondylous centra without irregularities, though from the middle to the rear of the caudal peduncle they become progressively longer. Diplospondyly begins slightly anterior to origin of pelvic fins. The $\frac{\text{length}}{\text{diameter}}$ of penultimate monospondylous centrum was 0.94-1.20 (mean 1.08) and the $\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}$ was 1.43-1.64 (mean 1.53) in 4 specimens.

The smallest specimen seen by me was the holotype, a male of 238 mm TL, while the largest was a female of 466 mm. If the holotype was free living (i.e., not an embryo), then it is likely that this species does not grow to more than about 700 mm TL. The smallest female examined, of 278 mm, had an obvious but closed yolk stalk scar, suggesting that it was recently born.

²⁶L. J. V. Compagno, Division of Systematic Biology, Stanford University, Stanford, CA 94305, pers. commun. September 1969.

Table 85.—*Carcharhinus borneensis*, proportional dimensions in percentage of total length.

	♀ 278 mm Borneo RMNH 7666	♂ 332 mm Sarawak BMNH 1895.2.28	♀ 466 mm China Chusan Is. SU 66750
Snout tip to			
outer nostrils	4.5	5.3	4.6
eye	8.0	8.6	7.9
mouth	8.4	8.9	8.7
1st gill opening	19.4	19.4	18.4
3d gill opening	21.7	22.0	—
5th gill opening	23.4	23.8	—
pectoral origin	23.0	23.5	21.9
pelvic origin	49.6	46.7	45.7
1st dorsal origin	31.7	31.6	30.7
2d dorsal origin	64.0	63.2	62.3
anal fin origin	61.5	60.6	60.4
upper caudal origin	74.8	74.4	73.4
lower caudal origin	73.4	72.9	72.4
Nostrils			
distance between inner corners	6.5	6.3	5.8
Mouth			
width	7.7	8.1	8.2
length	4.7	4.8	4.3
Labial furrow lengths			
upper	0.4	0.3	0.2
lower	0.5	0.6	0.6
Gill opening lengths			
1st	2.0	2.3	2.1
3d	2.5	2.9	—
5th	2.3	2.9	—
Eye			
horizontal diameter	2.6	2.3	2.1
1st dorsal fin			
length of base	10.2	9.6	10.1
length posterior margin	4.1	5.1	5.1
height	7.0	8.1	8.6
2d dorsal fin			
length of base	3.8	3.0	3.9
length posterior margin	4.0	4.5	4.7
height	1.8	2.0	1.9
Anal fin			
length of base	4.5	3.8	3.9
length posterior margin	3.4	4.2	3.9
height	2.3	2.7	2.8
Pectoral fin			
length of base	5.8	5.4	6.0
length anterior margin	12.9	13.5	14.1
length distal margin	8.3	9.6	10.5
greatest width	7.7	8.4	8.8
Pelvic fin			
length of base	4.1	4.5	4.5
length anterior margin	5.0	5.3	5.2
length distal margin	3.8	3.9	4.4
length of claspers	—	2.2	—
Caudal fin			
length of dorsal lobe	25.2	25.6	26.6
length of ventral lobe	10.8	10.7	10.9
Trunk at pectoral origin			
width	11.5	11.7	11.8
height	10.2	9.3	9.9
Dental formula	12-1-12 11-1-11	12-1-12 11-1-11	12-1-12 11-1-12
Vertebrae			
precaudal	61	62	63
caudal	57	56	58
total	118	118	121

Table 86.—Vertebral numbers in the holotype of *Carcharhinus (Prionodon) borneensis* plus range of vertebral numbers in *Carcharhinus borneensis*.

Specimens		Precaudal	Caudal	Total
RNH 7386	Borneo	62	52 +	114 +
Range (including counts from Table 85)		61-63	52 + -58	114 + -121

Distribution (see also Material examined).—Four of the five specimens examined were from Borneo and the fifth from China (Chusan Island, southeast of Shanghai). On the basis of these disparate localities *borneensis* could be expected to have a wide distribution in the tropical west Pacific. Giltay (1933) reported it from Java but his account is insufficient to confirm his identification.

Material examined.—RNH 7386, male, 238 mm [holotype of *Carcharias (Prionodon) borneensis*] Borneo, Singkawang; RNH 7666, female, 278 mm, Borneo, Pontianak, 1895, Moret; BMNH 1895.2.28, male, 332 mm, Borneo, Sarawak, H. H. Rajah Brooks; MSNG C.E. 23320, female, 407 mm, Borneo, 1887; SU 66750, female, 466 mm, China, Chusan Island, 1937, A. W. Herre.

ZOOGEOGRAPHY OF *CARCHARHINUS* SPECIES

The 25 species of *Carcharhinus* are predominantly tropical-subtropical fishes, reaching their greatest abundance in these warmer waters of the globe. However, many of them not infrequently extend into higher, temperate latitudes either as stragglers, seasonal visitors, or even regular inhabitants of warm-current systems. On present information only two species, *amblyrhynchoides* and *fitzroyensis*, are confined to the tropics, but the data on these, as on several other species, are too sparse to give any surety that this is their real distribution. By contrast, a further seven species, (*brachyurus*, *falciformis*, *longimanus*, *leucas*, *limbatus*, *obscurus*, *plumbeus*) have been recorded from the tropics to latitudes as high as 40° or more, although only one of them, *brachyurus*, could be regarded as having its center of abundance outside the tropics. The remaining 16 species have the outer limits of their distribution variably from about 25° to 35° latitude, with more than half of them at about lat. 30°.

Nearly all of the species are essentially coastal, inhabiting shelf waters or shallow rises and banks. Some are equally at home in the waters surrounding islands and atolls as they are along continental coastlines, but one species, *galapagensis*, is on present information virtually confined to waters in the vicinity of oceanic islands or rises. This distribution of *galapagensis* thus contrasts with that of *obscurus*, a species that although very similar to *galapagensis* is found mainly along continental coastlines. Only two species, *falciformis* and *longimanus*, can be said to be principally oceanic, open-sea dwellers, although even these, and particularly *falciformis*, may occur near shore at times. For *longimanus* these occurrences are mostly near to islands where the bordering shelf is narrow.

Only *leucas*, and possibly *amboinensis*, appear capable of, or show a tendency for, entry into water of reduced salinity. Records of other species from off the mouths of large rivers or in estuaries suggest that they may be able to tolerate brackish situations, but firm data are lacking, and there is the possibility, as noted for *limbatus* by Bass et al. (1973), that such estuarine occurrences may be associated with incoming tides of seawater. For *leucas*, however, there is ample and conclusive evidence from many parts of the world that it can spend considerable periods of time in brackish or even freshwater in estuaries, rivers, and lakes, but nowhere does it appear to be land-locked or confined to freshwater. Data for *amboinensis* are less il-

luminating, although Bass (see footnote 12) provided a record of a Western Australian specimen from brackish water, and there is further support for its occurrence in freshwater from specimens taken in the Fitzroy River, Queensland, Australia, and which appear on somewhat circumstantial evidence to be *amboinensis*.

Table 87 shows in broad scale how the 25 *Carcharhinus* species are distributed circumglobally, in terms of the four principal tropical shorefish regions. Eight species (32%) are worldwide, being present in all four regions, and as might be expected these are species whose members grow to a large size, up to at least 2.5 m long. However, this group does not contain several other large species, e.g., *albimarginatus* and *perezii*, which grow to about 3.0 m and *brevipinna* which reaches 2.8 m, and which have less extensive distributions. Eleven (44%) of the 25 species are present in at least 3 regions, and 13 (52%) occupy

Table 87.—*Carcharhinus* species in the four principal tropical shore fish regions. An X indicates that the species has been recorded from a region.

Species	Indo-Pacific	Eastern Pacific	Western Atlantic	Eastern Atlantic
<i>altimus</i>	X	X	X	X
<i>brachyurus</i>	X	X	X	X
<i>falciformis</i>	X	X	X	X
<i>galapagensis</i>	X	X	X	X
<i>leucas</i>	X	X	X	X
<i>limbatus</i>	X	X	X	X
<i>longimanus</i>	X	X	X	X
<i>obscurus</i>	X	X	X	X
<i>plumbeus</i>	X	?	X	X
<i>brevipinna</i>	X		X	X
<i>porosus</i>	X	X	X	
<i>albimarginatus</i>	X	X		
<i>amboinensis</i>	X			X
<i>amblyrhynchos</i>	X			
<i>amblyrhynchoides</i>	X			
<i>borneensis</i>	X			
<i>cautus</i>	X			
<i>dussumieri</i>	X			
<i>fitzroyensis</i>	X			
<i>melanopterus</i>	X			
<i>sealei</i>	X			
<i>sorrah</i>	X			
<i>wheeleri</i>	X			
<i>acronotus</i>			X	
<i>perezii</i>			X	
Total	23	10	13	11

at least 2 regions, leaving 12 (48%) which are restricted to 1 region. It is not surprising in view of the known richness of the Indo-Pacific fauna that 10 of these last-mentioned 12 species are, on present information, endemic to the Indo-Pacific region. The other two species (*acronotus* and *perezii*) are restricted to the western Atlantic. Neither the eastern Pacific nor the eastern Atlantic has any endemics.

The richness of the Indo-Pacific region is further emphasized by the fact that 23 of the 25 species or 92% are included within its boundaries. The other three regions are, by comparison, impoverished, the richest of them being the western Atlantic with 13 species (52%), while the eastern Atlantic and eastern Pacific have slightly lesser faunas of 11 species (44%) and 10 species (40%). From these values it can be concluded that the distribution of *Carcharhinus* species accords remarkably well with the overall picture of faunal numbers and diversity throughout these faunal regions.

Table 88 summarizes the distribution of the 23 Indo-Pacific species throughout that region. The boundaries of the five subregions are as described in Cohen's (1973) account of the zoogeography of Indian Ocean fishes. It must be emphasized again that the complement of species shown for the eastern Indian Ocean, western Pacific, and to a lesser extent the central Pacific, must be regarded as tentative because of inadequate collections and studies from those subregions. Much more confidence can be placed in the completeness of our knowledge of *Carcharhinus* from the Red Sea and western Indian Ocean due to the works of Gohar and Mazhar (1964), Fourmanoir (1961), and particularly Bass et al. (1973). The same can be said for the open-ocean fauna of the central Pacific (Strasburg 1958) and the nearshore fauna of the Hawaiian Islands (Tester see footnote 4), but for many other parts of the central Pacific details are fragmentary or lacking.

Inspection of Table 88 shows that only five species are common to all five subregions. Four of these species are large and worldwide or essentially so in their distribution (*falciformis*, *limbatus*, *longimanus*, *plumbeus*), but the fifth is the smaller, near-

shore *melanopterus*. Data on the number of species occupying a progressively lesser number of subregions fall into a very orderly sequence numerically. Thus following the above number of 5 species common to 5 subregions there are 10 species present in at least 4 subregions, 15 in at least 3 subregions, and 20 in at least 2 subregions. Only three species are restricted to one subregion, and all three of these (*borneensis*, *fitzroyensis*, *porosus*) are in the western Pacific.

An orderly sequence of occupancy is further demonstrated in Table 88 by the virtual symmetry of the data for the total number of species in each subregion when the subregions are arranged according to their normal geographical relationship. Thus the two peripheral subregions, the Red Sea and the central Pacific, have small and almost numerically equal faunas (10 and 9 species) whereas their adjacent subregions, the western Indian Ocean and western Pacific, have large faunas which again are almost numerically equal (19 and 21 species). The eastern Indian Ocean subregion with an intermediate-sized fauna of 14 (perhaps 15) species would appear to complement this symmetry, although reversing the trend for increasing numbers towards the center, but I suggest that the presently known difference between its fauna and that of the two adjacent subregions is illusory and due to inadequate collecting. It would be very surprising if species such as *albimarginatus*, *amblyrhynchoides*, *galapagensis*, and *altimus*, not yet recorded from the eastern Indian Ocean, do not, in fact, occur there. Their addition to the known fauna would leave little difference between the eastern and western Indian Ocean subregions. On the other hand, a slight but continuing difference between the eastern Indian Ocean and the western Pacific could be predicted in view of the novel elements of the latter fauna.

Few of the Indo-Pacific species have highly restricted distributions. The western Pacific is the only subregion with species endemic to it (*borneensis* and *fitzroyensis*) or not found elsewhere in the Indo-Pacific (*porosus*, also known from the eastern Pacific and western Atlantic). If adjacent subregions are linked, the Red Sea-western Indian Ocean have one endemic (*wheeleri*) and the eastern Indian Ocean-western Pacific have four (as for western Pacific above plus *cautus*). Most of the species are widespread, and the bulk of them (18 or 78%) are present from the western Indian Ocean to the western or central Pacific. All of the species common to the western and eastern Indian Ocean subregions also occur in the western Pacific.

Comparison of the above findings with those for some other fish groups in the Indo-Pacific (Cohen 1973) is complicated by the wide habitat diversity of *Carcharhinus* species. Thus although most of the species can be regarded as shelf fauna some of the smaller species such as *melanopterus* could be treated almost as shore fishes while other larger species are predominantly pelagic. Despite this and the small numbers of species in the fish groups so far sampled there is reasonable concordance with Cohen's findings, particularly with respect to the rather high proportion of species with widespread distributions, i.e., from the western Indian Ocean, to the western or central Pacific. For shorefishes Cohen described one category (based on some blenniids, gobioides, cirrhitids, and acanthurids) in which the widespread species made up 48% of the total, and noted that in studies by other authors on serranids 44% of the species were widespread. However, Cohen also described a second category of shorefishes (based on some blenniids, acanthurids, and antennariids) in which 85% of the members were widespread. For shelf fishes the two groups (triancanthoids and mugiloidids) dealt with by Cohen agreed with the first category

Table 88.—*Carcharhinus* species of the Indo-Pacific region. An X indicates that the species has been recorded from a subregion.

Species	Red Sea	Western Indian	Eastern Indian	Western Pacific	Central Pacific
<i>falciformis</i>	X	X	X	X	X
<i>limbatus</i>	X	X	X	X	X
<i>longimanus</i>	X	X	X	X	X
<i>melanopterus</i>	X	X	X	X	X
<i>plumbeus</i>	X	X	X	X	X
<i>brevipinna</i>	X	X	X	X	
<i>obscurus</i>	X	X	X	X	
<i>sorrah</i>	X	X	X	X	
<i>albimarginatus</i>	X	X		X	X
<i>wheeleri</i>	X	X			
<i>amblyrhynchos</i>		X	X	X	X
<i>amboinensis</i>		X	X	X	
<i>brachyurus</i>		X	X	X	
<i>dussumieri</i>		X	X	X	
<i>leucas</i>		X	X	X	
<i>amblyrhynchoides</i>		X	?	X	
<i>galapagensis</i>		X		X	X
<i>sealei</i>		X		X	
<i>altimus</i>		X			X
<i>cautus</i>			X	X	
<i>borneensis</i>				X	
<i>fitzroyensis</i>				X	
<i>porosus</i>				X	
Total	10	19	14	21	9

of shorefishes in that about half of the Indian Ocean species were widespread. These values span a range of 44-85% and thus embrace the value of 78% for *Carcharhinus* species. A comparable range of values of 55 and 92% obtains for the members of the two groups (belonids and clupeids) of tropical epipelagic fishes for which Cohen gives data.

Of the 21 species listed from the eastern Indian Ocean-western Pacific subregions, i.e., embracing the Indo-Australian Archipelago and Australia, only 16 of them (Table 89) are so far recorded from Australia itself. Considering the size of the Australian continent, its diversity of coastline, and the sizeable proportion of it which lies within the tropical zone, its fauna is disproportionately small. Further collecting will be necessary to establish what other species are present, but undoubtedly at least two additional species (*albimarginatus* and *falciformis*) which are wide ranging will be found to occur there. Only one species (*fitzroyensis*) has a distribution which on present information is limited to Australia itself.

The small number of species (5) in the Mediterranean (Table 90) is, at least at first sight, rather surprising, especially as the adjacent eastern Atlantic region has 11 species. Such a disparity is seemingly at odds with the situation for fishes as a whole in which the Mediterranean "... fauna is a good deal richer than that of the Atlantic coasts..." (Briggs 1974). Three possibilities suggest themselves to explain the disparity. Firstly, despite the long history of ichthyological endeavor in the Mediterranean the present species list may still be incomplete. Support for this comes from the fact that *brachyurus* as recorded here is a new listing, and from the long-standing proposals that other species including *longimanus* are present. Secondly, the history of the Mediterranean, and particularly the change from a tropical to a warm temperate regime between the early Tertiary and the Pliocene, coupled with the effects of Pleistocene glaciation, may have seen the extinction of essentially tropical species that once existed there. The opening of the Suez Canal in 1869 could have provided a subsequent means of ingress for such species—and *melanopterus* may be one of them that has populated it by that route and has found suitably warm conditions in the southern

Mediterranean at least—but this re-entry could be slow and limited by other ecological factors. Thirdly, there is the fact that the Mediterranean is warm temperate rather than tropical and this may be the main limiting factor. This could well explain why three of the five species there (*brachyurus*, *limbatus*, and *plumbeus*) belong in that group of seven species noted above as extending into high latitudes, i.e., more than lat. 40°, yet at the same time it is equally puzzling why the remaining four species (*falciformis*, *leucas*, *longimanus*, and *obscurus*) in that group are not also present insofar as they occur in the eastern Atlantic.

Some of the species whose range spans two or more zoogeographic regions also exhibit intraspecific variation throughout their range. The variation is either in the form of meristic differences particularly in vertebral numbers but to some extent in dental formulae, or in morphometric differences in such features as snout proportions, fin heights, etc., or in color differences mainly in terms of the degree and extent of dark or light fin tip markings. Where the populations of these species differ on each side of a geographic barrier of known duration, such as the Central American isthmus, it is tempting to calculate the rate of evolution of the difference on the assumption that there is a direct relationship between the amount of difference and the period of isolation of the populations. For the Central American barrier the two most appropriate species to consider in this context are *porosus* (which shows differences in vertebral number) and *limbatus* (differences in snout length and in black fin tip markings). However, taking *porosus* as an example, little confidence can be placed in the findings of such an exercise, because although eastern Pacific specimens with 62-67 precaudal vertebrae are clearly distinct from Atlantic Panama specimens with 53-57, and there are good estimates of the time since the most recent emergence of the barrier, other considerations throw doubt on a simple relationship between this divergence and the presence of the barrier. In particular, samples of *porosus* from Surinam and northern Brazil with 41-48 precaudal vertebrae and from southern Brazil with 53-56 precaudal vertebrae are as equally divergent from each other as are the ampho-American samples but this difference between them cannot be ascribed to a known physical barrier. A second consideration, as noted by Gilbert (1967) in his study of the Sphyrnidae, is that even if the Central American barrier is of prime significance as an isolating mechanism it is possible that its effects date back further than the period since its most recent

Table 89.—*Carcharhinus* species of the eastern Indian-western Pacific subregions and of Australia.

Species	Eastern Indian-Western Pacific	Australia
<i>albimarginatus</i>	X	
<i>amblyrhynchoides</i>	X	X
<i>amblyrhynchos</i>	X	X
<i>amboinensis</i>	X	X
<i>borneensis</i>	X	
<i>brachyurus</i>	X	X
<i>brevipinna</i>	X	X
<i>cautus</i>	X	X
<i>dussumieri</i>	X	
<i>falciformis</i>	X	
<i>fitzroyensis</i>	X	X
<i>galapagensis</i>	X	X
<i>leucas</i>	X	X
<i>limbatus</i>	X	X
<i>longimanus</i>	X	X
<i>melanopterus</i>	X	X
<i>obscurus</i>	X	X
<i>plumbeus</i>	X	X
<i>porosus</i>	X	
<i>sealei</i>	X	X
<i>sorrah</i>	X	X
Total	21	16

Table 90.—*Carcharhinus* species of the eastern Atlantic, Mediterranean and Red Sea.

Species	Eastern Atlantic	Mediterranean	Red Sea
<i>brevipinna</i>	X	X	X
<i>limbatus</i>	X	X	X
<i>plumbeus</i>	X	X	X
<i>brachyurus</i>	X	X	
<i>falciformis</i>	X		X
<i>longimanus</i>	X		X
<i>obscurus</i>	X		X
<i>altimus</i>	X		
<i>amboinensis</i>	X		
<i>galapagensis</i>	X		
<i>leucas</i>	X		
<i>melanopterus</i>		X	X
<i>albimarginatus</i>			X
<i>sorrah</i>			X
<i>wheeleri</i>			X
Total	11	5	10

Pliocene) emergence. In view of the likely geological age of *Carcharhinus* species this is eminently possible, and hence nullifies any simple attempt at calculating evolutionary rates.

Although the above-mentioned intraspecific differences in some species appear to be of little use for interpreting or estimating evolutionary rates, they may in the future be shown to have some value, in another context, in tracing the source of some of the Mediterranean fauna. It has been suggested by various authors (Ben-Tuvia 1966) that following the opening of the Suez Canal in 1869 the Mediterranean fauna was augmented by immigrants from the Red Sea. *Carcharhinus* species included in this category have been *brevipinna* and *melanopterus*. Alternatively these species may be part of the original Mediterranean-Mediterranean-eastern Atlantic fauna which was overlooked or not found by the early workers on it. Present data for *brevipinna* from the Mediterranean, Red Sea, and eastern Atlantic are few, and no clear differences are apparent between them, although comparison of vertebral numbers between the eastern Atlantic and western North Atlantic populations show very marked differences. For *melanopterus* I have no data on Mediterranean specimens, and I treat it as a member of that fauna only on the listings by several authors including Quignard and Capapé (1971a) and Capapé (1975). Of the other three species of *Carcharhinus* now known to be in the Mediterranean (*plumbeus*, *limbatus*, and *brachyurus*), none has been suggested as a Red Sea immigrant, and in fact *brachyurus* has not been reported from the Red Sea although it is common to the south in the western Indian Ocean. Meristic and morphological data which might show the relationships of the Mediterranean members of these species are inadequate for all three of them. However, *plumbeus* was described from the Mediterranean well before the opening of the Suez Canal, and hence must be regarded as a primary element of the Mediterranean fauna. Its pre-1869 presence in the Mediterranean is further supported by two of the probable syntypes of *milberti* (= *plumbeus*) which were collected from Italian waters prior to the description of *milberti* in 1841 and which are still in existence in the Berlin and Leiden museums. For *brachyurus* the evidence is less clear-cut, but the Vienna Museum contains specimens collected from the Mediterranean coast of France (Nice) in 1881 and 1889.

Four species pairs of *Carcharhinus* can be recognized (Table 1) in which the members of each pair are so similar that they can reasonably be regarded as sibling species. In three of these pairs the two members are clearly sympatric throughout their range; in the fourth pair (*amblyrhynchus-wheeleri*) the evidence for sympatry is meager, comprising only Bass et al.'s (1973) record of one specimen of *amblyrhynchus* from the western Indian Ocean (off Madagascar) where *wheeleri* is common. In two pairs one member has a worldwide distribution (*limbatus* and *leucas*) and the second member is either Indo-

Pacific (*amblyrhynchoides*) or predominantly Indo-Pacific (*amboinensis* which is also known from the eastern Atlantic from Krefft's (1968) record of one specimen from Nigeria). The other two pairs are both Indo-Pacific, with one member of each predominating in the western Indian Ocean (*sealei* and *wheeleri*) and the other in the Indo-Australian Archipelago (*dussumieri*) and central Pacific (*amblyrhynchus*).

SPECIES DUBIA

I am unable to identify the following 13 nominal species, although from their descriptions and other circumstantial evidence it is likely that they belong in *Carcharhinus* or other related genera.

Carcharias brachyrrhynchus Philippi, 1887:540-541, pl.1, fig. 1. Female, 2.48 m, Chile, Iquique.

Eulamia philippi Fowler, 1930:491. Proposed as new name for *Carcharias brachyrrhynchus* Philippi, 1887 because the latter was thought to be preoccupied by *Carcharias (Prionodon) brachyrrhynchus* Bleeker, 1856.

The sole specimen used by Philippi (1887) for his description of *brachyrrhynchus* lacked jaws, but despite this Philippi thought it belonged in *Carcharias* because of the shape of the caudal fin. His illustration of *brachyrrhynchus* shows the caudal fin with a prominent terminal lobe, suggestive of *Galeorhinus*, but the large size of the specimen makes it unlikely to have been a species of that genus. In general the illustration is stylized, and although it is unlikely that much confidence can be placed in its detail, there is no doubt that it is of a carcharhinid shark and probably *Carcharhinus*. The proportional dimensions given by Philippi, and his description, do not permit identification of the species. I do not know if the type specimen is still in existence.

Fowler's (1930:491) proposal to replace the name *brachyrrhynchus* with the new name *philippi* is not valid because *brachyrrhynchus* Philippi, 1887 and *brachyrrhynchus* Bleeker, 1856 are not homonyms. Fowler (1930) did not provide any new data but only suggested that *philippi* was "Possibly allied with the Atlantic *Eulamia obscura* (LeSueur) and *Eulamia porosa* (Ranzani) in the second dorsal smaller than the anal and its origin little posterior." Agreement between *philippi* (*brachyrrhynchus*) and *obscura* is feasible, but this would not be possible for *porosus* which is a small species.

Prionodon cucuri Castelnau, 1855:99. No specimens mentioned; Bahia, Brazil.

Castelnau ascribed the specific name *cucuri* to Marcgrave (1648:164) and in so doing obviously intended it to be a senior

Table 9L.—Distribution of *Carcharhinus* species-pairs.

	Red Sea	Western Indian	Eastern Indian	Western Pacific	Central Pacific	Eastern Pacific	Western Atlantic	Eastern Atlantic	Mediterranean
<i>leucas</i>		X	X	X		X	X	X	
<i>amboinensis</i>		X	X	X				X	
<i>limbatus</i>	X	X	X	X	X	X	X	X	X
<i>amblyrhynchoides</i>		X	?	X					
<i>amblyrhynchus</i>		X	X	X	X				
<i>wheeleri</i>	X	X							
<i>dussumieri</i>		X	X	X					
<i>sealei</i>		X		X					

synonym of *limbatus* (Valenciennes in Müller and Henle, 1841) which he cited. However, Marcgrave's account is pre-Linnean, hence Castelnau is the author of *cucuri*. Castelnau's description of *cucuri* is extremely brief and other than noting that *cucuri* reaches a length of 1 m, is used for food, and is common from October to February, refers only to the color of the species. The significant statements about the color are that the first dorsal fin is bordered with black, the second dorsal is black tipped, and the anal is gray, bordered with black.

This description is not definitive. It possibly could be interpreted as referring to *brevipinna* or to *limbatus*, in which case it would have been based on juvenile specimens, or conceivably even to *acronotus* or *porosus*, all four of which are known from Brazil. Reference to Marcgrave's account is not helpful for the illustration there is ludicrously unreal, and the description conflicts with that of Castelnau's in that it states that all the fins are ash-gray except the smaller ones (pelvic and anal) on the lower side of the body, which are white.

Duméril (1865:375, footnote 2) noted that in the Paris Museum there was a specimen of *cucuri*, 370 mm long, which had been sent from Bahia by Castelnau; this specimen resembled *limbatus* in all features except that the teeth in both jaws were very oblique, and the upper teeth were strongly notched on their lateral margins; Duméril tentatively assigned *cucuri* to *limbatus* but questioned whether it represented a different species. I do not know if the specimen which Duméril mentioned is still in existence, but even if it is not, some interpretations can be made from Duméril's information on it. Firstly, if the specimen was only 370 mm long, yet had its teeth erupted sufficiently for Duméril to describe their shape, it could not be either *brevipinna* or *limbatus* because of its small size, or because of the obliqueness of its teeth. Secondly, the shape of the teeth, particularly of the uppers, could fit either *acronotus* or *porosus*. However, it is likely that *porosus* can be discounted because the posterior position of its second dorsal fin relative to its anal fin is a distinctive character that would have been noted by Duméril. This leaves *acronotus* as the best contender—it has many similarities to *limbatus*, is of the right order of size, has the apex of the second dorsal fin black margined or dusky (but no dark marks on the first dorsal or anal such as Castelnau described for *cucuri*) and has oblique and notched upper teeth. However, to synonymize *cucuri* and *acronotus* on this evidence would be extremely speculative and improper in respect to the fact that *cucuri* could preempt the later and well-described *acronotus*. Nomenclature would be better served by disregarding the name *cucuri*.

Galeolamna greyi Owen, 1853:96.

Owen's account of *greyi* is very brief and was probably not intended as a description. In total it reads as follows: "No. 427. The upper and lower jaws of a shark (*Galeolamna Greyi*) from South Australia; the teeth in the upper jaw resemble those of the *Galeus*; those of the lower jaw are intermediate between the teeth of *Lamna* and *Carcharias*. Presented by Governor Grey."

The brevity of the account and the essential lack of description are such that *Galeolamna greyi* could well be regarded as a nomen nudum, and this decision seems to have been taken by subsequent authors including Duméril (1865), Günther (1870), and Garman (1913) who omitted any reference to it. However, Whitley (1932) accepted *Galeolamna greyi* as available and

discussed or utilized the specific name *greyi* in several accounts (1934, 1939, 1940, 1945, 1967) as well as making more general use of the generic name *Galeolamna*. The name *greyi*, including also three subspecies of it described by Whitley (1945), has thus intruded into the Australian literature.

Owen's (1853) account allows no interpretation of the species and the type material on which it was based—a pair of jaws in the Museum of the Royal College of Surgeons, England—was lost as a result of bomb damage in World War II. However, Whitley, who had examined the jaws, published (1939) a brief description of them and later (1967) a photograph. Whitley also kindly gave me a copy of the notes and sketches he had made when he examined the jaws. This information leaves no doubt that *greyi* belongs in *Carcharhinus*. The dental formula of the

type was $\frac{15-2-15}{15-2-15}$. The upper teeth were broadly triangular

erect to slightly oblique, with shallowly notched lateral margins and straight to slightly convex medial margins; both margins were serrated, and according to Whitley's notes the serrations were somewhat coarser basally on the lateral margins. The lower teeth were erect, narrow, and apparently finely serrated toward their tips, though the serrations could only be felt rather than seen. The gape of the jaws was about 195 mm.

Examination of Table 4 shows that nine species of *Carcharhinus* have a dental formula encompassing the $\frac{15-2-15}{15-2-15}$ of

the type of *greyi*. Differences in tooth shape exclude most of these species from consideration, leaving *obscurus* and *falciformis* as the two most likely contenders. Both reach an appropriate size to match the jaws of *greyi* (the gape of the type would suggest that the shark was in the order of 2 m long). Although there is no record that I am aware of that *falciformis* is present in Australia, let alone southern Australia, I do not regard this as compelling evidence for excluding *falciformis* from consideration. Its wide distribution in other oceans suggests that it will be found to occur off Australia too. The shape of the upper teeth of *greyi*, with their shallow lateral notch and coarser serrations basally, and in some cases an incipient medial notch, resembles that of *falciformis*, as does also the virtual smoothness of the lower teeth. However, in general the teeth appear somewhat too large for *falciformis*. Their size is more appropriate for *obscurus*, but 2 m long specimens of that species have upper teeth with concave rather than notched lateral margins.

The above findings leave me unable to firmly identify *greyi* but, provided I am correct in limiting the identity of *greyi* to either *obscurus* or *falciformis*, then failure to decide between these two will not have any affect on nomenclature since both predate *greyi*. The same could not be said if *brachyurus* were involved, as this is a later name dating from Günther (1870). Whitley's determinations of *greyi* wavered in his various accounts (Garrick 1962a) but mostly favored *brachyurus*. However, although *brachyurus* agrees with *greyi* in dental formula and size, and is present in southern Australia, its upper teeth are markedly narrower, smaller, and of a different shape.

Of the three subspecies of *greyi* which Whitley (1945) proposed, *greyi greyi* appears referable to *brachyurus* judging by dental formula and Whitley's illustration of an upper tooth (the illustration of the whole shark is not convincing in proportions and detail but could have been based on *brachyurus*), *greyi mckaili* is conspecific with *leucas* (see p. 81), and *greyi cauta* is recognized here as a valid species (see p. 102).

Carcharias falcipinnis Lowe, 1839:90. No reference to type specimens, only that this shark "... is about three feet [914 mm] long, and the female differs in nothing from the male." hence indicating that more than one specimen was seen; Madeira.

Lowe's description, in Latin, is brief, and I am unable to identify the species from it, though significant features are: the snout is short, broad, depressed, and blunt; the first dorsal fin is high and placed somewhat forward of or above the middle of the pectoral fins; the pectorals are long, narrow, and falcate with blunted tips; and the second dorsal and anal fins are opposite each other. The shark is described as very rare.

Lowe tentatively referred it to *Squalus ustus* Duméril [= *Carcharhinus melanopterus* (Quoy & Gaimard)] and noted that its teeth are "precisely similar to those of the Tintureira (*C. glaucus*, Cuv.)" [= *Prionace glauca* (Linn.)].

In a later account, Lowe (1843:93) noted that his *C. falcipinnis* "proves, as it was suspected, to be the *Squalus ustus*, Dum.; that is, *Charcharias* (*Prionodon*) *melanopterus* (Q. & G.) of MM. Müller and Henle."

Insofar as *melanopterus* does not occur in the Atlantic, Lowe's identification must be set aside. Günther (1870:366) followed this course and synonymized *falcipinnis* with *Carcharhinus obscurus* (Lesueur, 1818), presumably on the basis of two specimens in the British Museum, which he listed as from Madeira and presented by Lowe. One of these, which Günther noted as "c. Stuffed, 40 inches [1,016 mm] long. Madeira. Presented by the Rev. R.T. Lowe" may be the same as a mounted skin (No. 840) which I have examined and which is labelled as a probable syntype of *Carcharias falcipinnis* Lowe 1839, and is a male, about 950 mm long, bearing the British Museum catalogue number 1851.4.9.14. This specimen is clearly referable to *Carcharhinus falciformis* (Bibron in Müller and Henle, 1841). If the status of this specimen as a type of *C. falcipinnis* was established definitely, then the name *falcipinnis* would have priority over *falciformis*. However, unequivocal evidence of its type status does not appear to be available. I have not been able to find any other type material of *falcipinnis*.

In view of the above information, i.e., an insufficiently diagnostic description, lack of definite type material, and the fact that the identity of the supposed type material could provide a threat to the well-established name *falciformis*, I propose that the virtually unused name *falcipinnis* Lowe, 1839 be disregarded.

Hypoprion ? Hemigaleus ? heterodus Philippi, 1887:541-542, pl. 2, fig. 6. Jaws only, the lower jaw with a "circunferencia" of 52 cm; Chile.

The description of *heterodus* by Philippi (1887:541) is inadequate for identification, being based only on a large pair of jaws in the Museo Nacional de Historia Natural, Chile. The accompanying illustrations of a few of the teeth leave little doubt that *heterodus* belonged in *Carcharhinus* rather than in either *Hypoprion* or *Hemigaleus*, to both of which Philippi provisionally referred it. The dental formula $\left(\frac{14-14}{14-2-14} \right)$, the shape of the upper teeth (broadly triangular, oblique and concave but not notched on their lateral margins), and the size of the jaws suggest *obscurus* or possibly *galapagensis* rather than any other species. Philippi's description of the third series

of upper symphyseal teeth having a truncated cusp carrying three or four cusplets is undoubtedly due to their being damaged, even though Philippi considered and rejected this possibility. I do not know if the holotype of *heterodus* is still available.

Hypoprion ? Hemigaleus ? isodus Philippi, 1887:542, pl. 2, fig.

5. Jaws only, the upper jaw with a "circunferencia" of 35 cm; Chile.

I am unable to identify *isodus* which Philippi (1887:542) described only from a set of jaws in the Museo Nacional de Historia Natural, Chile. Compared with *heterodus*, which Philippi also described from jaws in the same account, *isodus* differed in having no upper symphyseal teeth, narrower upper teeth, narrower based lower teeth, and larger lower symphyseal

teeth. The dental formula was apparently $\frac{14-14}{14-2-14}$. The teeth

appear to be from a species of *Carcharhinus*, judging by Philippi's illustrations, though the lack of upper symphyseal teeth is an unusual feature and would exclude those species which otherwise agree in dental formula and upper tooth shape. *Prionace glauca* frequently lacks an upper symphyseal tooth, but the upper teeth of *isodus*, as illustrated, seem too broad for that species. Examination of the type material, if still available, is needed if the identity of *isodus* is to be established.

Carcharias Javanicus Van Hasselt, 1823:315. No type material mentioned; Java.

For discussion of this nomen dubium see under my account of *dussumieri*, p. 59.

Carcharias (*Prionodon*) *munsing* Bleeker, 1849:16. One specimen, 401 mm long; sea at Madura, near Kammal and Surabaya.

Bleeker's (1849:16) first description of *munsing* listed only one small specimen from Madura, to the northeast of Java, and is quite brief and general. The species is not identifiable from this account though certain features in the description seem distinctive. These are that the first dorsal fin was low (about 8% TL), the pectoral fin short (its length about 14% TL), the second dorsal fin larger than the anal, and the fins were gray with no mention of white or dark tips. The upper teeth were simply described as serrated, and the lower teeth narrow and smooth. In a later account Bleeker (1852:32) amplified his description of *munsing*, this time basing it on two specimens, male and female, of 390 and 401 mm, from Madura. This extended description does not clearly fit any *Carcharhinus* that I have seen, and makes *munsing* appear even more distinctive in having the first dorsal fin nearer to the pelvic fins than to the pectorals. Bleeker made particular note of this character by using it as a primary key item, by repeating it in the description itself, and by referring to it in comments under the description where he likened it to the condition in the blue shark, *Prionace glauca*. Amongst *Carcharhinus* species this condition is most nearly matched in *borneensis* Bleeker (1858-59), but that species differs from *munsing* in several features including the upper teeth which are quite unlike those in Bleeker's (1852) illustration of the snout and mouth. This was his only published illustration of *munsing* and shows the upper teeth as broadly triangular, and erect or at most slightly oblique, which agrees with his (1852)

description as "triangularibus parum obliquis, totis denticulatis." In his comments under this description he noted that the stomachs of both specimens contained fish, thus indicating that they were already free living despite their small size of 390 and 401 mm. This means that *munsing* was a small species, unlikely to exceed about 1.5 m TL, and possibly less depending on how long his specimens had been free living. These two specimens now appear to have been lost.

The only other information available on *munsing* is in an unpublished Bleeker Atlas in the Leiden Museum, which includes on plate 13 an excellent colored illustration labelled as that species, plus insets of the head and teeth. Unfortunately these illustrations only add confusion because they cannot adequately be reconciled with the descriptions of *munsing*, and are not necessarily drawn from either of the two specimens Bleeker listed in 1852. Although there is agreement in many features (fin sizes, shapes, and positions, and particularly the first dorsal fin being set far back so that its rear tip is about level with the pelvic origin whereas its origin is just anterior to the inner corner of the pectoral fin), the snout is much longer and more pointed than in the 1852 illustration, the eye is too large to be "oculis diametro 6 in longitudine rostro," and the upper teeth are markedly different, being narrower, very oblique and with deep notches laterally. These discrepancies show that two species were involved. Even if the unpublished illustrations are of one of the two specimens which Bleeker (1852) listed, I cannot establish whether they are of the holotype which he had earlier described in 1849 or of the second specimen which he had included in 1852. Nor for that matter can I unequivocally refer these illustrations to any *Carcharhinus* species, although they show many similarities to *fitzroyensis* Whitley, 1943. Because of these uncertainties I see no opportunity of resolving the identity of *munsing*, and hence treat it as a species dubium.

Carcharias Murrayi Günther, 1883:137. One specimen, 6 ft 8 in, 6 lines (2,044 mm); India, Kurrachee (= Karachi).

Günther (1883:137) based his description of *murrayi* on one specimen about 2.0 m long obtained from Karachi. This holotype, originally deposited in the British Museum, cannot now be found. Several features of Günther's description show that *murrayi* was *leucas*-like. In particular the snout was short and obtuse, the preoral length was less than the internarial width, the teeth (as figured in Günther where they are the only illustration given for *murrayi*) were approximately of the right shape, the first dorsal fin originated above or slightly behind the pectoral axil, and the second dorsal fin was in front of the anal. However, other items in the description suggest that *murrayi* cannot be interpreted as *leucas*; these include smooth-edged lower teeth, 29 teeth across the lower jaw, and a second dorsal fin which was "conspicuously larger than the anal, which is small." No other species of *Carcharhinus* has, in total, the characteristics of *murrayi*. The possibility remains, nevertheless, that *murrayi* has more affinity with the species which Müller and Henle (1841) described as *Carcharias (Prionodon) gangeticus* and *C. (Pr.) glyphis* but which are excluded here from *Carcharhinus*. In both of these species the second dorsal fin is notably larger than the anal, and in *gangeticus* the lower teeth (as illustrated in Müller and Henle) have a lateral cusplet on one or both sides of the major cusp similar to that shown in Günther's illustration of *murrayi*. It is worth noting too, that both *gangeticus* and *glyphis* were described from the Indian

continent, with *gangeticus* coming from freshwater (Ganges River) as may well have been the case with *murrayi* from Karachi which is on the delta of the Indus River.

Carcharias robustus Philippi, 1896:389-390. One specimen, 2,920 mm long; eastern tropical Pacific.

Philippi's (1896:389) description of *robustus* from one large specimen from the eastern tropical Pacific was not accompanied by an illustration, and I do not know if the type still exists. The description is fairly general but is almost certainly that of a *Carcharhinus* judging by the teeth (triangular, finely serrated on their margins, the largest 23 mm tall) and the proportional dimensions. The shark was named *robustus* because of its stout body which Philippi likened to that of *Lamna huidobrii* (= *Isurus oxyrinchus*). Comparison of some features was made with *brachyrrhynchus* Philippi (1887) but this does not assist me in identifying *robustus* because I am likewise unable to identify *brachyrrhynchus*. However, the size of the type, combined with it having a short snout and an anal fin of about the same size as the second dorsal and situated underneath that fin, suggest that *robustus* could be identified as the much later described *galapagensis* Snodgrass and Heller (1905), but such identification would be very speculative.

Carcharias sancti-thomae Engelhardt, 1912:646. One female, 1,000 mm; four heads, 160-180 mm; West Indies, St. Thomas.

The description of *sancti-thomae* (which name should be corrected to *sanctithomae*) is fairly brief and comprises only a comparison with features of *sorrah* which are also listed. Important items are that *sanctithomae* had oblique, serrated, and laterally notched teeth, a long snout, and lacked black fin tips. The two Caribbean species of *Carcharhinus* most likely to fit this description are *acronotus* and *porosus*. If comparison is limited to these two species, then Engelhardt's statement that the distal margin of the first dorsal fin is much less concave than that of *sorrah*, and almost straight, would apply better to *porosus* than *acronotus*. However, *porosus* has not been recorded from the islands of the Caribbean, though it is present on the adjacent continental coastline. On the other hand, *acronotus* occurs at the Caribbean islands, but it has a dusky to black-tipped second dorsal fin, which is contrary to Engelhardt's description of *sanctithomae*. In view of these discrepancies I am unable to identify *sanctithomae* with confidence. I do not know if type material still exists.

Carcharias (Prionodon) siamensis Steindachner, 1896:229-230. Male, 630 mm, Irrawady River, near Rangoon.

Steindachner's (1896:229) description of *siamensis* is fairly extensive and contains a reasonable amount of detail, but despite that I am unable to identify his species. The account was not illustrated, and I do not know if the type is still in existence. Some features of the description suggest a similarity to *leucas*, as for example, the short, broad, bluntly rounded snout, the small eye, and second dorsal fin slightly larger than the anal fin and originating a little in front of it, and the statement that the distance between the dorsal fins is $3\frac{1}{4}$ times the length of the second dorsal base. The suggestion is enhanced by the fact that the type was from the mouths of the Irrawaddy near Rangoon,

which could mean that it was living in brackish or freshwater. However, Steindachner gave *siamensis* a dental formula of $\frac{29}{29}$, which is just outside the range for *leucas*, and he introduced an element of confusion by stating that a line between the inner ends of the nostrils lies almost two times nearer to the snout end than to the mouth—a relationship which does not occur in any species of *Carcharhinus*. Furthermore his measurement of the length of the eye (4.4 mm) would mean that the eye was only 0.7% TL which is impossibly small for a specimen of *leucas* 630 mm long. In view of these discrepancies I see no possibility of firmly identifying *siamensis* on presently available information.

Carcharhinus watu Setna and Sarangdhar, 1946:252. No specimens mentioned; India, Bombay.

The only information pertaining to *watu* in the original account of that species by Setna and Sarangdhar (1946) is contained in a key to the sharks and rays of Bombay waters. There is no illustration. Of the two couplets which encompass *watu* in the key the first states that the "Tips of pectorals and lower lobe of caudal black" while the second describes the teeth and gives a dental formula ($\frac{14-3-14}{14-0-14}$). I cannot identify *watu* from these data, but the teeth as described are unusual, notably the uppers ("oblique, externally notched; serrations only on notches and opposite basal margins; cusps flattened and non-serrated"). The smooth-edged distal parts of the cusps suggest the possibility that *watu* was a species of *Hypoprion* rather than *Carcharhinus*; it could, perhaps, have been *H. hemiodon* which occurs in Indian waters (not mentioned by Setna and Sarangdhar (1946) though they include *H. maculoti* in their key) and which would agree with *watu* in having black-tipped fins.

ACKNOWLEDGMENTS

This study would not have been possible without the assistance of very many colleagues who contributed in various ways, including making available specimens from their collections and facilities to examine them, arranging for radiographing, providing data and literature, and helping with translations. I would wish to mention all of these individually but fear that in so doing I might inadvertently omit some, and hence I take the easier course of thanking them all in general. They include staff members of those museums and institutions which provided material and which I list under that heading, plus many others who contributed outside those sources and are acknowledged where possible throughout the text.

Above all I wish to acknowledge the role of Leonard P. Schultz, former Curator of Fishes, Smithsonian Institution, who envisaged this study and made the arrangements which made it possible for me to work on it at that institution for 3 yr (September 1960-December 1963). His assistance, encouragement, and advice are much appreciated. I thank also my colleagues at that institution, and likewise those at the Australian Museum, Sydney, where I continued with it in 1969 and at the National Museum, Wellington, in 1976.

Financial support for the study was provided by contracts between the Smithsonian Institution and the Atomic Energy Commission (AEC [30-1] 2409) and the Office of Naval Research

(NONR 1354 [09]), and by grants from the National Science Foundation (GB-245), the Tropical Fish Hobbyist Fund (Smithsonian Institution), the Trustees of the Australian Museum, and the Internal Research Fund, Victoria University of Wellington.

The drawings of shark teeth are by Peter A. McCrery, and those of the adult specimen of *C. cautus* by J. A. Bass. The graphs and some of the tables are by K. Hicks and the photographs in Plate I by J. Benfield. The final typing of the manuscript was by Norma Knuckey to whom I owe a special note of gratitude for her meticulous skill.

I would like to thank also those colleagues who aided me greatly with advice and discussion throughout the course of this study; in particular I would mention J. A. Bass, L. J. V. Compagno, Jeannette D. D'Aubrey, S. Springer, and V. G. Springer. Finally I am grateful for the tolerance and patience shown by all who have assisted in this study and have had to wait so long for its completion.

LITERATURE CITED

- ABELLA, A.
1972. Hallazgo de una nueva especie de *Carcharhinus*, en la Costas de Rocha, Uruguay. Bol. Soc. Zool. Urug. 2:102-106.
- AGASSIZ, J. L. R.
1843. Recherches sur les poissons fossiles. Vol. 3, 390 p. Petit-pierre, Neuchatel.
- ALCOCK, A.
1890. Natural history notes from H.M.'s Indian Marine Survey Steamer "Investigator," Commander Alfred Carpenter, R.N., D.S.O., Commanding, No. 14. Observations on the gestation of some sharks and rays. J. Asiat. Soc. Bengal 59(1):51-56.
- BACKUS, R. H.
1957. Notes on western North Atlantic sharks. Copeia 1957:246-248.
- BACKUS, R. H., S. SPRINGER, and E. L. ARNOLD.
1956. A contribution to the natural history of the white-tip shark, *Pterolamiops longimanus* (Poey). Deep-Sea Res. 3:178-188.
- BANE, G. W., Jr.
1966. Observations on the silky shark, *Carcharhinus falciformis*, in the Gulf of Guinea. Copeia 1966:354-356.
- BARANES, A., and A. BEN-TUVIA.
1978. Occurrence of the sandbar shark *Carcharhinus plumbeus* in the northern Red Sea. Isr. J. Zool. 27:45-51.
- BASS, A. J.
1973. Analysis and description of variation in the proportional dimensions of scyliorhinid, carcharhinid and sphyrnid sharks. S. Afr. Assoc. Mar. Biol. Res., Invest. Rep. 32, 28 p.
- BASS, A. J., J. D. D'AUBREY, and N. KISTNASAMY.
1973. Sharks of the east coast of southern Africa. I. The genus *Carcharhinus* (Carcharhinidae). S. Afr. Assoc. Mar. Biol. Res., Invest. Rep. 33, 168 p.
1975. Sharks of the east coast of southern Africa. III. The families Carcharhinidae (excluding *Mustelus* and *Carcharhinus*) and Sphyrnidae. S. Afr. Assoc. Mar. Biol. Res., Invest. Rep. 38, 100 p.
- BAUGHMAN, J. L.
1942. A shark new to the fauna of the United States. Copeia 1942:188.
1943. Note on the Texas occurrence of a shark not previously known from the waters of the United States. Copeia 1943:189.
- BEEBE, W., and J. TEE-VAN.
1933. Field book of the shore fishes of Bermuda. G.P. Putnam's Sons, N.Y., 337 p.
1941. Eastern Pacific Expeditions of the New York Zoological Society. XXV. Fishes from the tropical eastern Pacific. [From Cedros Island, Lower California, south to the Galapagos Islands and northern Peru.] Part 2. Sharks. Zoologica (N.Y.) 26:93-122.
- BENNETT, E. T.
1831. Characters of new genera and species of fishes from the Atlantic Coast of northern Africa, presented by Captain Belcher, R.N. Proc. Zool. Soc. Lond. 1830-31(1):148.
- BEN-TUVIA, A.
1953. Mediterranean fishes of Israel. Bull. Sea Fish. Res. Stn., Caesarea 8, 40 p.

1966. Red Sea fishes recently found in the Mediterranean. *Copeia* 1966:254-275.
- BERTIN, L.
1939. Catalogue des types de poissons du Muséum National d'Histoire Naturelle. 1^{re} Partie. Cyclostomes et Sélaciens. Bull. Mus. Natl. Hist. Nat., 2^e sér., 11:51-98.
- BIGELOW, H. B., and W. C. SCHROEDER.
1944. New sharks from the western North Atlantic. *Proc. New Engl. Zool. Club* 23:21-36.
1948. Fishes of the western North Atlantic. *Mem. Sears Found. Mar. Res., Yale Univ.*, Part 1, 576 p.
1961. *Carcharhinus nicaraguensis*, a synonym of the bull shark, *C. leucas*. *Copeia* 1961:359.
- BIGELOW, H. B., W. C. SCHROEDER, and S. SPRINGER.
1943. A new species of *Carcharhinus* from the western Atlantic. *Proc. New Engl. Zool. Club* 22:69-74.
- BINI, G., and E. TORTONESE.
1955. Missione sperimentale di pesca nel Cile e nel Peru. Pesci marini Peruviani. Boll. Pesca Piscic. Idrobiol. 9:151-185.
- BLAINVILLE, H. M. D. de.
1816. Prodrome d'une nouvelle distribution systématique de règne animal. Bull. Sci. Soc. Philomat. Paris 8:113-124.
1825. Poissons. In L. P. Vieillot, Faune Française ou histoire naturelle, générale et particulière des animaux qui se trouvent en France, p. 1-96. Plassan, Paris.
- BLEEKER, P.
1849. Bijdrage tot de kennis der ichthyologische fauna van het Eiland Madura, met beschrijving van eenige nieuwe soorten. Verh. Bataviaasch genoot. Kunsten Wet. 22(8):1-16.
1852. Bijdrage tot de kennis der plagiostomen van den Indischen Archipel. Verh. Bataviaasch genoot. Kunsten Wet. 24(12):1-92.
1853. Diagnostische beschrijvingen van nieuwe of weinig bekende vischsoorten van Batavia. Natuur. Tijdschr. Ned. Indië 4:451-516.
1854. Vijde bijdrage tot de kennis der ichthyologische fauna van Amboina. Natuur. Tijdschr. Ned. Indië 6:455-508.
1856. *Carcharias Prionodon amblyrhynchos*, eene nieuwe haaisort, gevangen nabij het Eiland Solombo. Natuur. Tijdschr. Ned. Indië 10:467-468.
1858-59. Twaalfde bijdrage tot de kennis der vischfauna van Borneo. Vijschen van Sinkawang. Acta Soc. Sci. Indo-Neerl. 5:1-10.
1861. Mededeeling omtrent vischsoorten, nieuw voor de kennis der fauna van Singapoera. Versl. Meded. K. Akad. Wet. 12:28-63.
- BLEGVAD, H.
1944. Fishes of the Iranian Gulf. Dan. Sci. Invest. Iran Part III, 247 p.
- BOESEMANN, M.
1960. A tragedy of errors: the status of *Carcharhinus* Blainville, 1816; *Galeolamna* Owen, 1853; *Eulamia* Gill, 1861; and the identity of *Carcharhinus commersonii* Blainville, 1825. *Zool. Meded. (Leiden)* 37:81-100.
1964. Notes on the fishes of western New Guinea. III. The fresh water shark of Jamoer Lake. *Zool. Meded. (Leiden)* 40:9-22.
- BÖHLKE, J.
1953. A catalogue of the type specimens of recent fishes in the Natural History Museum of Stanford University. *Stanford Ichthyol. Bull.* 5:1-168.
- BONHAM, K.
1960. Note on sharks from Rongelap Atoll, Marshall Islands. *Copeia* 1960:257.
- BRADLEY, J. T.
1940. The history of Seychelles. Vol. 2, Description of its geology, flora, fauna, fishes, crabs, marine Mollusca, butterflies, land and freshwater Mollusca. Its religion, climate, political prisoners and health conditions. Also a description of the islands of the archipelago, exports, imports, population, manufactures, guano and distilleries, p.174-465. [Not seen.]
- BRIGGS, J. C.
1974. Marine zoogeography. McGraw-Hill, N.Y., 475 p.
- BRYAN, P. G.
1973. Three new shark records from Guam, Mariana Islands. *Micronesica* 9:159-160.
- CADENAT, J.
1937. Liste des poissons littoraux avec la diagnose préliminaire de 6 espèces nouvelles. *Rev.Trav. Off. Peches Marit.* 10:423-562.
1950. Poissons de mer du Sénégal. *Inst. Fr. Afr. Noire Initiations Afr.* 3, 345 p.
1957. Notes d'ichthyologie ouest-africaine XVII. Biologie. Régime alimentaire. *Bull. Inst. Fr. Afr. Noire, Ser. A, Sci. Nat.* 19:274-294.
1961. Notes d'ichthyologie ouest-africaine XXXIV. Liste complémentaire des espèces de poissons de mer (provenant des côtes de l'Afrique occidentale) en collection à la section de biologie marine de l'I.F.A.N. à Gorée. *Bull. Inst. Fr. Afr. Noire, Ser. A, Sci. Nat.* 23:231-245.
- CAPAPÉ, C.
1975. Sélaciens nouveaux et rares le long des côtes Tunisiennes. Premières observations biologiques. *Arch. Inst. Pasteur Tunis* 52(1-2):107-128.
- CASTELNAU, F. de.
1855. Animaux nouveaux ou rares recueillis pendant l'expédition dans les parties centrales de l'Amérique du Sud, de Rio de Janeiro à Lima, et de Lima au Para; exécutée par Ordre du Gouvernement Français pendant les années 1843 à 1847, ... Poissons. P. Bertrand, Paris, 112 p.
- CERVIGON, F.
1966. Los peces marinos de Venezuela. *Fund. La Salle Cienc. Nat. Caracas, Monogr.* 11, 436 p.
1968. Los peces marinos de Venezuela. Complemento 1. *Mem. Soc. Cienc. Nat. La Salle* 28:177-218.
- CHEN, J. T. F.
1963. A review of the sharks of Taiwan. *Biol. Bull. Dep. Biol., Coll. Sci., Tunghai Univ., Ichthyol. Ser.* 1, 19, 102 p.
- CHURCH, R.
1961. Shark attack. *Skin Diver Mag.* 10(11):30-31.
- CLARK, E.
1975. Into the lairs of "sleeping" sharks. *Natl. Geogr. Mag.* 147:571-584.
- CLARK, E., and K. VON SCHMIDT.
1965. Sharks of the central Gulf Coast of Florida. *Bull. Mar.Sci.* 15:13-83.
- COHEN, D. M.
1973. Zoogeography of the fishes of the Indian Ocean. In B. Zeitzschel (editor), *The biology of the Indian Ocean*, p. 451-463. *Ecol. Stud., Anal. Synth.*
- COMPAGNO, L. J. V.
1970. Systematics of the genus *Hemistriaks* (Selachii:Carcharhinidae), and related genera. *Proc. Calif. Acad. Sci., Ser. 4*, 38:63-97.
1973a. Interrelationships of living elasmobranchs. In P. H. Greenwood, R. S. Miles, and C. Patterson (editors), *Interrelationships of fishes*, p. 15-61. *Suppl. 1, Zool. J. Linn. Soc.*
1973b. *Carcharhinidae*. In J. C. Hureau and T. Monod (editors), *Check-list of the fishes of the north-eastern Atlantic and of the Mediterranean*. [In Engl. and Fr.] Vol. 1, p. 23-31. *Unesco, Paris.*
- D'AUBREY, J. D.
1964. Preliminary guide to the sharks found off the east coast of South Africa. *S. Afr. Assoc. Mar. Biol. Res., Invest. Rep.* 8, 95 p.
- DAY, F.
1873. On some new fishes of India. *J. Linn. Soc., Zool.* 11:524-530.
1878. The fishes of India; being a natural history of the fishes known to inhabit the seas and fresh waters of India, Burma, and Ceylon. Vol. 1, 778 p., Vol. 2, p. 779-816. *Bernard Quaritch, Lond.*
- DE KAY, J. E.
1842. *Zoology of New York, or the New-York fauna. Part IV. Fishes.* D. Appleton & Co. and Wiley & Putnam, N.Y., 415 p.
- DOUBILET, D.
1975. Rainbow world beneath the Red Sea. *Natl. Geogr. Mag.* 148:344-365.
- DUMÉRIL, A. H. A.
1865. Histoire naturelle des poissons ou ichthyologie générale. Vol. 1, Elasmobranches, 720 p. *Librairie Encyclopédia de Roret, Paris.*
- DUPONT, R.
1935. Conférence de M. Rivalz Dupont sur l'Archipel des Seychelles, sa formation géologique, ses ressources naturelles, sa flore, sa faune entomologique, et son évolution économique. *Trans. R. Soc. Arts Sci. Mauritius* 1933 and 1934:50-149. [Not seen.]
- ENGELHARDT, R.
1912. Über einige neue Selachier-Formen. *Zool. Anz.* 39:643-648.
- ERDMAN, D. S.
1956. Recent fish records from Puerto Rico. *Bull. Mar. Sci. Gulf Caribb.* 6:315-340.
- FANG, P. W., and K. F. WANG.
1932. The elasmobranchiate fishes of Shangtung coast. *Contrib. Biol. Lab. Sci. Soc. China, Zool. Ser.* 8:213-283.
- FELLOWS, D. P., and A. E. MURCHISON.
1967. A noninjurious attack by a small shark. *Pac. Sci.* 21:150-151.
- FIRTH, F. E.
1931. Some marine fishes collected recently in New England waters. *Bull. Boston Soc. Nat. Hist.* 61:8-14.
- FOURMANOIR, P.
1961. Requins de la cote Ouest de Madagascar. *Mém. Inst. Sci. Madagascar, Sér. F Océanogr.*, 4:3-81.
1964. Raies et Requins-scie de la cote Ouest de Madagascar (ordre des Batoidei). *Cah. O.R.S.T.O.M. Océanogr.* 6(Sér. NOSY-BE 11):33-58.
- FOWLER, H. W.
1905. Some fishes from Borneo. *Proc. Acad. Nat. Sci. Phila.* 57:455-523.
1928. The fishes of Oceania. *Mem. Bernice P. Bishop Mus.* 10, 540 p.
1930. A list of the sharks and rays of the Pacific Ocean. *Proc. 4th Pac. Sci.*

- Congr. 3:481-508.
1932. The fishes obtained by the Pinchot South Seas Expedition of 1929, with description of one new genus and three new species. *Proc. U.S. Natl. Mus.* 80(6), 16 p.
1938. The fishes of the George Vanderbilt South Pacific Expedition, 1937. *Monogr. Acad. Nat. Sci. Phila.* 2, 349 p.
1941. Contributions to the biology of the Philippine Archipelago and adjacent regions. The fishes of the groups Elasmobranchii, Holocephali, Isospondyli, and Osteophyti obtained by the United States Bureau of Fisheries steamer "Albatross" in 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. *U.S. Natl. Mus. Bull.* 100(13), 879 p.
1944. The fishes. In *Results of the Fifth George Vanderbilt Expedition (1941)*. (Bahamas, Caribbean Sea, Panama, Galápagos Archipelago and Mexican Pacific Islands.) *Monogr. Acad. Nat. Sci. Phila.* 6:57-529.
1959. Fishes of Fiji. Government of Fiji, Suva, 670 p.
- GARMAN, S.
1913. The Plagiostomia. (Sharks, skates, and rays). *Mem. Mus. Comp. Zool. Harvard Coll.* 36, 515 p.
- GARRICK, J. A. F.
- 1962a. Reasons in favour of retaining the generic name *Carcharhinus* Blainville, and a proposal for identifying its type species as the Indo-Pacific black-tipped shark, *C. melanopterus*. *Proc. Biol. Soc. Wash.* 75:89-96.
- 1962b. *Carcharhinus* Blainville, 1816 (class Chondrichthyes, order Selachii); proposed designation of *Carcharias melanopterus* Quoy & Gaimard as type-species under the plenary powers. *Z.N.(S.)920. Bull. Zool. Nomencl.* 19:100-102.
1967. A broad view of *Carcharhinus* species, their systematics and distribution. In P. W. Gilbert, R. F. Mathewson, and D. P. Rall (editors), *Sharks, skates, and rays*, p. 85-91. The Johns Hopkins Press, Baltimore.
- GARRICK, J. A. F., R. H. BACKUS, and R. H. GIBBS, JR.
1964. *Carcharhinus floridanus*, the silky shark, a synonym of *C. falciformis*. *Copeia* 1964:369-375.
- GILBERT, C. H.
1892. Scientific results of explorations by the U. S. Fish Commission steamer Albatross. No. XXII.—Descriptions of thirty-four new species of fishes collected in 1888 and 1889, principally among the Santa Barbara Islands and in the Gulf of California. *Proc. U.S. Natl. Mus.* 14:539-566.
- GILBERT, C. H., and E. C. STARKS.
1904. The fishes of Panama Bay. *Mem. Calif. Acad. Sci.* 4, 304 p.
- GILBERT, C. R.
1967. A revision of the hammerhead sharks (family Sphyrnidae). *Proc. U.S. Natl. Mus.* 119(3539), 88 p.
- GILBERT, P. W., and D. A. SCHLERNITZAUER.
1965. Placentation in the silky shark, *Carcharhinus falciformis*, and bonnet shark, *Sphyrna tiburo*. *Anat. Rec.* 151:452.
1966. The placenta and gravid uterus of *Carcharhinus falciformis*. *Copeia* 1966:451-457.
- GILL, T.
1862. Analytical synopsis of the order of *Squali*; and revision of the nomenclature of the genera. *Ann. Lyceum Nat. Hist. N.Y.* 7:367-408.
- GILL, T., and J. F. BRANSFORD.
1877. Synopsis of the fishes of Lake Nicaragua. *Proc. Acad. Nat. Sci. Phila.*, Ser. 3, 29:175-191.
- GILTAY, L.
1933. Poissons. *Mém. Mus. R. Hist. Nat. Belg.*, Hors sér. 5(3), 129 p.
- GLOVER, C. J. M.
1974. The whitetip oceanic shark *Pterolamiops longimanus* (Poey) 1861 - a first record from off the southern Australian coast. *S. Aust. Nat.* 49(1):12-13.
- GOHAR, H. A. F., and F. M. MAZHAR.
1964. The elasmobranchs of the north-western Red Sea. *Publ. Mar. Biol. Stn. Al-Ghardaqa (Red Sea)* 13:3-144.
- GUIART MANDAY, D.
1968. Guía para los tiburones de aguas cubanas (con notas adicionales sobre los del Golfo de México, Mar Caribe y Océano Atlántico cerca de Cuba). *Acad. Cienc. Cuba, Ser. Oceanol.* 1, 61 p.
- GÜNTHER, A.
1870. Catalogue of the fishes of the British Museum. Vol. 8, 549 p. Br. Mus., Lond.
1880. Report on the shore fishes procured during the voyage of H.M.S. Challenger in the years 1873-1876. *Rep. Sci. Results Voyage H.M.S. Challenger, Zool.* 1(6):1-82.
1883. Notes on some Indian fishes in the collection of the British Museum. *Ann. Mag. Nat. Hist.*, Ser. 5, 11:137-140.
1889. Report on the pelagic fishes collected by H.M.S. Challenger during the years 1873-76. *Rep. Sci. Results Voyage H.M.S. Challenger, Zool.* 31(2):1-47.
1910. Andrew Garrett's *Fische der Südsee*, beschrieben und redigiert von Albert C. L. G. Günther, J. Mus. Godeffroy 6:389-515.
- HEMPRICH, F. G., and C. G. EHRENBERG.
1899. In F. Hügendorf (editor), *Symbolae Physicae . . . , Zoologica, Pisces*, p. 7-10. Berlin.
- HERRE, A. W. C. T.
1934. Notes on fishes in the Zoological Museum of Stanford University. I. The fishes of the Herre Philippine Expedition of 1931. Hong Kong, 106 p.
1936. Fishes of the Crane Pacific Expedition. *Field Mus. Nat. Hist., Zool. Ser.* 21:1-472.
- HESS, P. W.
1962. Notes on some sharks in the western North Atlantic and Bahama areas. *Copeia* 1962:653-656.
- HILDEBRAND, S. F.
1946. A descriptive catalog of the shore fishes of Peru. *U.S. Natl. Mus. Bull.* 189, 530 p.
- HOOIJER, D. A.
1954. Pleistocene vertebrates from Celebes. IX. Elasmobranchii. *Proc. K. Ned. Akad. Wet., Ser. B Phys. Sci.*, 57:475-485.
- HORNELL, J.
1927. Report on the fisheries and fish resources of the Seychelles Islands, 76 p. [Not seen.]
- HUBBS, C. L.
1951. Record of the shark *Carcharhinus longimanus* accompanied by *Naukrates* and *Remora*, from the east-central Pacific. *Pac. Sci.* 5:78-81.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE.
1950. The official record of Proceedings of the International Commission on Zoological Nomenclature at their session held in Paris in July 1948. *Bull. Zool. Nomencl.* 4:269-271, 283-287.
1965. Opinion 723. Repeal of the ruling given in Opinion 47 together with the stabilisation of the generic names *Carcharhinus* Blainville, 1816, *Carcharodon* Smith, 1838, and *Odontaspis* Agassiz, 1838, in their accustomed sense (Pisces). *Bull. Zool. Nomencl.* 22:32-36.
- JORDAN, D. S., and B. W. EVERMANN.
1896. The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. *U.S. Natl. Mus. Bull.* 47:1-1240.
1898. The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. *U.S. Natl. Mus. Bull.* 47:2183a-3136.
1904. Descriptions of new genera and species of fishes from the Hawaiian Islands. *Bull. U.S. Fish Comm.* 22:161-208.
1905. The aquatic resources of the Hawaiian Islands. Part 1.—The shore fishes. *Bull. U.S. Fish Comm.* 23 (part 1), 574 p.
- JORDAN, D. S., and C. H. GILBERT.
- 1883a. Description of four new species of sharks from Mazatlan, Mexico. *Proc. U.S. Natl. Mus.* 5:102-110.
- 1883b. Description of a new shark (*Carcharias lamiella*) from San Diego, California. *Proc. U.S. Natl. Mus.* 5:110-111.
- KATO, S.
1964. Sharks of the genus *Carcharhinus* associated with the tuna fishery in the eastern tropical Pacific Ocean. *U.S. Fish Wildl. Serv., Circ.* 172, 22 p.
- KATO, S., and A. H. CARVALLO.
1967. Shark tagging in the eastern Pacific Ocean, 1962-65. In P. W. Gilbert, R. F. Mathewson, and D. P. Rall (editors), *Sharks, skates, and rays*, p. 93-109. The Johns Hopkins Press, Baltimore.
- KATO, S., S. SPRINGER, and M. H. WAGNER.
1967. Field guide to eastern Pacific and Hawaiian sharks. *U.S. Fish Wildl. Serv., Circ.* 271, 47 p.
- KENNEDY, G. R.
1975. Plankton of the Fitzroy River Estuary, Queensland: (1) the upper reaches. *Proc. R. Soc. Queensl.* 86:163-171.
- KLAUSEWITZ, W.
1959. Ergebnisse der Xarifa-Expedition 1957/58 des Instituts für Submarine Forschung, Vaduz (Leitung: Dr. H. Hass). *Fische aus dem Roten Meer. I. Knorpelfische (Elasmobranchii)*. *Senckenb. Biol.* 40:43-50.
1960. Die Typen und Typoide des Naturhistorischen Museums Senckenberg, 23: Pisces, Chondrichthyes, Elasmobranchii. *Senckenb. Biol.* 41:289-296.
- KLUNZINGER, C. B.
1871. Synopsis der fische des Rothen Meeres. II. Theil. *Verh. Zool.-Bot. Ges. Wein.* 21:441-688.
- KREFFT, G.
1954. Ichthyologische Mitteilungen aus dem Institut für Seerfischerei der Bundesforschungsanstalt für Fischerei III. 5. Ergänzungen zur Haifauna Perus. *Zool. Anz.* 153:41-48.
1968. Knorpelfische (Chondrichthyes) aus dem tropischen Ostasien. *Atl.*

- Rep. 10:33-76.
- LACÉPEDE, B. G. E. de la V.
1798. Histoire naturelle des poissons. Vol. 1, 532 p. Paris.
- LAHILLE, F.
1928. Nota sobre unos peces Elasmobranchios. An. Mus. Nac. Hist. Nat. Bernardino Rivadavia B. Aires 34:299-339.
- LESSON, R. P.
1830. Zoologie. In L. Duperrey, Voyage autour du monde, exécuté par ordre du roi, sur la corvette de la majesté, *La Coquille*, pendant les années 1822, 1823, 1824 et 1825. Vol. 2, pt. 1, 471 p. Arthus Bertrand, Paris.
- LESUEUR, C. A.
1818. Descriptions of several new species of North American fishes. J. Acad. Nat. Sci. Phila. 1:222-235.
1822. Description of a *Squalus*, of a very large size, which was taken on the coast of New Jersey. J. Acad. Nat. Sci. Phila. 2:343-352.
- LIMBAUGH, C.
1963. Field notes on sharks. In P. W. Gilbert (editor), Sharks and survival, p. 63-94. D. C. Heath and Co., Boston.
- LINDSEY, C. C.
1975. Pleomerism, the widespread tendency among related fish species for vertebral number to be correlated with maximum body length. J. Fish. Res. Board Can. 32:2453-2469.
- LOWE (McCONNELL), R. H.
1962. The fishes of the British Guiana continental shelf, Atlantic Coast of South America, with notes on their natural history. J. Linn. Soc. Lond., Zool. 44:669-700.
- LOWE, R. T.
1839. A supplement to a synopsis of the fishes of Madeira. Proc. Zool. Soc. Lond. 7:76-92.
1840. On new species of fishes from Madeira. Proc. Zool. Soc. Lond. 8:36-39.
1843. Notices of fishes newly observed or discovered in Madeira during the years 1840, 1841, and 1842. Proc. Zool. Soc. Lond. 11:81-95.
- McCOY, F.
1867. On the recent zoology and palaeontology of Victoria. Ann. Mag. Nat. Hist., Ser. 3, 20:175-202.
- McCULLOCH, A. R.
1921. Notes on, and descriptions of Australian fishes, No. 2. Proc. Linn. Soc. N. S. W. 46:457-472.
- McKAY, R. J.
1970. Additions to the fish fauna of Western Australia—5. West. Aust. Dep. Fish. Fauna Fish. Bull. 9(5), 24 p.
- MARCGRAVE, G.
1648. In G. Pisonis, De Medicina Brasiliensi, 122 p., et G. de L. Marcgravi, Historiae Rerum Naturalium Brasiliae, 293 p. Ioannes de Laet, Antwerp.
- MARSHALL, T. C.
1964. Fishes of the Great Barrier Reef and coastal waters of Queensland. Angus and Robertson, Sydney, 566 p.
- MARTENS, E. V.
1876. Die Preussische Expedition nach Ost-Asien, Vol. 1, 412 p. Verlag der Königl. Geheinen Ober-Hofbuchdruckerei (R. V. Decker), Berlin. [Not seen.]
- MATHER, F. J., III, and C. G. DAY.
1954. Observations of pelagic fishes of the tropical Atlantic. Copeia 1954:179-188.
- MAUL, G. E.
1955. Five species of rare sharks new for Madeira including two new to science. Notulae Naturae (Phila.) 279, 13 p.
- MEEK, S. E., and S. F. HILDEBRAND.
1923. The marine fishes of Panama. Field Mus. Nat. Hist. Publ. 215, Zool. Ser. 15:1-330.
- MELOUK, M. A.
1957. On the development of *Carcharinus melanopterus* (Q. & G.). Publ. Mar. Biol. Stn. Al Ghardaq (Red Sea) 9:229-251.
- MENEZES, R. S. de.
1966. Some morphometric data on shark embryos. Arq. Estac. Biol. Mar. Univ. Fed. Ceará 6:143-146.
- MIRANDA-RIBEIRO, A. de.
1923. Peixes. Fauna Brasileira, Vol. 2, pt. 1a, p. 1-50b. [The plates are listed as "vol. 1 fasc. 1." Mus. Nac. Rio de Janeiro. [Not seen.]
- MOREAU, E.
1881. Histoire naturelle des poissons de la France. Vol. 1, 478 p. G. Masson, Paris.
1891. Histoire naturelle des poissons de la France. Supplément, 144 p. G. Masson, Paris.
- MÜLLER, J., and J. HENLE.
1841. Systematische beschreibung der plagiostomen. Von Veit and Co., Berlin, 200 p.
- MUNRO, I. S. R.
1955. The marine and fresh water fishes of Ceylon. Halstead Press, Sydney, 351 p.
- MYERS, G. S.
1952. Sharks and sawfishes in the Amazon. Copeia 1952:268-269.
- NAKAMURA, H.
1936. Report on a survey of the sharks of Taiwan. Rep. Taiwan Gov.-Gen. Fish. Exp. Stn. 7(1):1-54. [In Jpn. Engl. translations of the title of the article and the journal vary somewhat, and in some citations the word "Formosa" is substituted for "Taiwan."]
- NARDO, J. D.
1827. Prodrômus observationum et disquisitionum ichthyologiae Adriaticae. Oken's Isis 20(6):472-631.
1847a. Prospetto della fauna marine volgare del Veneto Estuario con cenni sulle principali specie commestibili dell'Adriatico, ecc. Venezia, 45 p.
1847b. Sinonimia moderna delle specie registrate nell'opera intitolata: Descrizione de' Crostacei, de' Testacei e de' Pesci che abitano le Lagune e Golfo Veneto rappresentati in figure, a chiaroscuro ed a colori dall'Abate Stefano Chierighini ven clodiense applicata per commissione governativa dal Dr Gio Domenico Nardo. Parte terza. Indice dei Pesci della Laguna e Golfo Veneto, p. 108-127. Venezia.
1853. Sopra due specie di Pesci pubblicate come nuove dal Prof. R. Molin osservazioni del dott. G. D. Nardo, Venezia, 16 p.
- OGILBY, J.
1910. On new or insufficiently described fishes. Proc. R. Soc. Queensl. 23:1-55.
1911. Descriptions of new or insufficiently described fishes from Queensland waters. Ann. Queensl. Mus. 10:36-58.
1915. Ichthyological notes (No. 2.). Mem. Queensl. Mus. 3:130-136.
1916. Check-list of the cephalochordates, selachians, and fishes of Queensland. Part 1. Mem. Queensl. Mus. 5:70-98.
- OWEN, SIR RICHARD
1853. Descriptive catalogue of the osteological series contained in the Museum of the Royal College of Surgeons of England. Vol. 1, 350 p. Taylor and Francis, Lond.
- PETERS, W. C. H.
1852. Hr. Peters legte einige neue Säugethiere und Flussfische aus Mossambique vor. Ber. Bekanntmachung geeigneten Verh. Königl. Preuss. Akad. Wiss. Berl., p. 273-276.
1868. Naturwissenschaftliche Reise nach Mossambique auf befehl seiner majestät des Königs Friedrich Wilhelm IV in den Jahren 1842 bis 1848 ausgeführt. Zoologie IV. Flussfische, 116 p.
- PHILIPPI, R. A.
1887. Sobre los Tiburones i algunos otros peces de Chile. An. Univ. Chile (Santiago) (Mem. Cient. Lit.) 71:535-563 + Append. p. 565-574.
1896. Peces nuevos de Chile. An. Univ. Chile (Santiago) (Mem. Cient. Lit.) 93-95:375-390.
- PHILLIPPS, W. J.
1924. A review of the elasmobranch fishes of New Zealand: No. 1. N.Z. J. Sci. Technol. 6:257-269.
- PIETSCHMANN, V.
1913. Fische des Wiesbadener Museums. Jahrb. Nassau. Ver. Nat. 66:171-201.
- POEY, F.
1858-61. Memorias sobre la historia natural de la Isla de Cuba, acompanadas de sumarios latinos y extractos en francés, Vol. 2, 442 p. Viuda de Barcina, Habana.
1865-66. Repertorio físico-natural de la Isla de Cuba, Vol. 1, 420 p. Gobierno y Capitanía general por S.M., Habana.
1866-68. Repertorio físico-natural de la Isla de Cuba, Vol. 2, 484 p. Viuda de Barcina, Habana.
1876. Enumeratio piscium cubensium. An. Soc. Esp. Hist. Nat. Madrid 5:131-218.
- POLL, M.
1949. Poissons. In Résultats scientifiques des croisières du navire-école Belge "Mercator." Mém. Inst. R. Sci. Nat. Belgique, Sér. 2, 33:173-269.
1951. Poissons. Expéd. Océanogr. Belge Eaux côtières Afr. Atl. Sud (1948-1949). Résult. Sci. 4(1), 154 p.
- QUIGNARD, J.-P., and C. CAPAPÉ.
1971a. Liste commentée des Selaciens de Tunisie. Bull. Inst. Natl. Sci. Tech. Océanogr. Pêche Salammbô 2:131-141.
1971b. Etude du nombre de vertèbres chez trente et une espèces de Selaciens des cotes de Tunisie. Bull. Inst. Natl. Sci. Tech. Océanogr. Pêche Salammbô 2:157-162.

- QUOY, J. R. C., and P. GAIMARD.
1824. Zoologie. In L. de Freycinet, Voyage autour du monde exécuté sur les corvettes de S.M. l'Uranie et la Physicienne, pendant les années 1817, 1818, 1819, et 1820, 712 p. Pillet Aîné, Paris.
- RAFINESQUE, C. S.
1810. Indice d'ittologia siciliana. Messina, 70 p.
- RAMSAY, E. P., and J. D. OGILBY.
1887a. On an undescribed shark from Port Jackson. Proc. Linn. Soc. N.S.W., Ser. 2, 2:163-164.
1887b. Note in Correction of certain errors in previous papers. Proc. Linn. Soc. N.S.W., Ser. 2, 2:1024.
- RANDALL, J. E.
1955. Fishes of the Gilbert Islands. Atoll Res. Bull. 47, 243 p.
1963a. A fatal attack by the shark *Carcharhinus galapagensis* at St. Thomas, Virgin Islands. Caribb. J. Sci. 3:201-205.
1963b. Dangerous sharks of the western Atlantic. In P. W. Gilbert (editor), Sharks and survival, p. 339-361. D. C. Heath and Co., Boston.
1973. Expedition to Pitcairn. Oceans 6(2):12-21.
1974. Rapa and beyond. Oceans 7(6):24-31.
- RANDALL, J. E., and G. S. HELFMAN.
1973. Attacks on humans by the blacktip reef shark (*Carcharhinus melanopterus*). Pac. Sci. 27:226-238.
- RANZANI, C.
1840. De novis speciebus piscium. Acad. Sci. Inst. Bononiensis, Novi comment. 4:65-83.
- READ, K. R. H.
1969. Pacific reef sharks. Aquasphere 4:12-16. [Not seen.]
- REY, L. L.
1928. Fauna Ibérica. Peces. Vol. 1, 629 p. Mus. Nac. Cienc. Nat., Madrid.
- RICHARDSON, J.
1843. List of fish hitherto detected on the coasts of New Zealand. In E. Dieffenback, Travels in New Zealand; with contributions to the geography, geology, botany, and natural history of that country, Vol. 2, p. 206-228. John Murray, Lond.
- ROCHEBRUNE, A. T. de
1882. Faune de la Sénégambie. Poissons. Actes Soc. Linn. Bord. 36, ser. 4, tome 6, p. 23-190. [Not seen.]
- ROSENBLATT, R. H., and W. J. BALDWIN.
1958. A review of the eastern Pacific sharks of the genus *Carcharhinus*, with a redescription of *C. malpeloensis* (Fowler) and California records of *C. remotus* (Duméril). Calif. Fish Game 44:137-159.
- RÜPPELL, E.
1835-38. Neue wirbelthiere zu der fauna von Abyssinien Gehörig. Fische des Rothen Meeres. Siegmund Schmerber, Frankfurt am Main, 148 p.
- SADOWSKY, V.
1967a. Selachier aus dem Litoral von Sao Paulo, Brasilien. Beitr. Neotrop. Fauna 5:71-88.
1967b. The adult stage of the shark *Carcharhinus remotus* (Duméril, 1865). Senckenb. Biol. 48:327-334.
1971. Notes on the bull shark *Carcharhinus leucas* in the lagoon region of Cananéia, Brazil. Bol. Inst. Oceanogr. São Paulo 20(2):71-78.
- SCHUCK, H. A., and J. R. CLARK.
1951. Record of a white-tipped shark, *Carcharhinus longimanus*, from the northwestern Atlantic. Copeia 1951:172.
- SCHULTZ, L. P.
1953. Class Chondrichthyes: cartilaginous fishes. In L. P. Schultz and collaborators, Fishes of the Marshall and Marianas Islands, p. 2-22. U.S. Natl. Mus. Bull. 202, Vol 1.
- SCHWARTZ, F. J.
1959. Two eight-foot cub sharks, *Carcharhinus leucas* (Müller and Henle), captured in Chesapeake Bay, Maryland. Copeia 1959:251-252.
1960. Additional comments on adult bull sharks *Carcharhinus leucas* (Müller and Henle), from Chesapeake Bay, Maryland. Chesapeake Sci. 1:68-71.
- SCOTT, E. O. G.
1942. Observations on some Tasmanian fishes. Part V. Pap. Proc. R. Soc. Tasmania 1941:45-54.
- SEALE, A.
1910. Fishes of Borneo, with descriptions of four new species. Philipp. J. Sci., Ser. D, 5:263-289.
- SETNA, S. B., and P. N. SARANGDHAR.
1946. Selachian fauna of the Bombay waters. Proc. Natl. Inst. Sci. India 12(5):243-259.
- SIVASUBRAMANIAM, K.
1969. New evidences on the distribution of predatory pelagic sharks in the tuna grounds of the Indian Ocean. Bull. Fish. Res. Stn. Ceylon 20:65-72.
- SMITH, J. L. B.
1951. A new galeorhinid shark from South Africa, with notes on other species. Ann. Mag. Nat. Hist., Ser. 12, 4:86-93.
1952a. Two chondrichthyan fishes new to South Africa. Ann. Mag. Nat. Hist., Ser. 12, 5:760-765.
1952b. *Carcharhinus zambezensis* Peters, 1852, with notes on other chondrichthyan fishes. Ann. Mag. Nat. Hist., Ser. 12, 5:857-863.
1957. Deep-line fishing in northern Mozambique, with the description of a new pentapodid fish. Ann. Mag. Nat. Hist., Ser. 12, 10:121-124.
1958a. Sharks of the genus *Pterolamiops* Springer, 1951 with notes on isurid sharks. Dep. Ichthyol., Rhodes Univ., Grahamstown, Ichthyol. Bull. 10:131-134.
1958b. The mystery killer, the new shark *Carcharhinus vanrooyeni*. Veld Vlei 3(9):12-14.
1961. Bronze whaler shark of Australia comes to South Africa. Field Tide 4(1):28.
- SMITH, J. L. B., and M. M. SMITH.
1963. The fishes of Seychelles. Dep. Ichthyol., Rhodes Univ., Grahamstown, 215 p.
- SNODGRASS, R. E., and E. HELLER.
1905. Papers from the Hopkins-Stanford Galapagos Expedition, 1898-1899. XVII. Shore fishes of the Revillagigedo, Clipperton, Cocos and Galapagos Islands. Proc. Wash. Acad. Sci. 6:333-427.
- SNYDER, J. O.
1904. A catalogue of the shore fishes collected by the steamer *Albatross* about the Hawaiian Islands in 1902. Bull. U.S. Fish Comm. 22:513-538.
- SPRINGER, S.
1938. Notes on the sharks of Florida. Proc. Fla. Acad. Sci. 3:9-41.
1940. The sex ratio and seasonal distribution of some Florida sharks. Copeia 1940:188-194.
1950. A revision of North American sharks allied to the Genus *Carcharhinus*. Am. Mus. Novit. 1451, 13 p.
1951. Correction for "A revision of North American sharks allied to the genus *Carcharhinus*." Copeia 1951:244.
1960. Natural history of the sandbar shark *Eulamia milberti*. U.S. Fish Wildl. Serv., Fish. Bull. 61, 38 p.
- SPRINGER, V. G.
1964. A revision of the carcharhinid shark genera *Scoliodon*, *Loxodon*, and *Rhizoprionodon*. Proc. U.S. Natl. Mus. 115:559-632.
- SPRINGER, V. G., and J. A. F. GARRICK.
1964. A survey of vertebral numbers in sharks. Proc. U.S. Natl. Mus. 116:73-96.
- STEAD, D. G.
1938. The "Bronze whaler." An undescribed Australian shark. Aust. Nat. 10(3):98-105.
- STEINDACHNER, F.
1867. Ichthyologische notizen (VI.) Sitzungsber. Math.-Naturwiss. Cl. Kais. Akad. Wiss. Wien 56(1):307-376.
1896. Bericht für die während der reise Sr. Maj. Schiff "Aurora" von Dr. C. Ritter V. Mierszowski in den Jahren 1895 und 1896 gesammelten fische. Ann. K.-K. Naturhis. Hofmuseums Wien 11:197-230.
- STRASBURG, D. W.
1958. Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. U.S. Fish Wildl. Serv., Fish. Bull. 58:335-361.
- TANG, D. S.
1934. The elasmobranchiate fishes of Amoy. Nat. Sci. Bull. Univ. Amoy 1(1):1-110. [Not seen.]
- TANIUCHI, T.
1971. Reproduction of the sandbar shark, *Carcharhinus milberti*, in the East China Sea. [In Engl., Jpn. summ.] Jpn. J. Ichthyol. 18:94-98.
- TEMMINCK, C. J., and H. SCHLEGEL.
1850. Fauna Japonica, Pisces. Part 6, p. 270-324. A. Arnes et Socios, Lugduni Batavorum.
- TESHIMA, K., and K. MIZUE.
1972. Studies on sharks. I. Reproduction in the female sumitsuki shark *Carcharhinus dussumieri*. Mar. Biol. (Berl.) 14:222-231.
- THOMERSON, J. E., and T. B. THORSON.
1977. The bull shark, *Carcharhinus leucas*, from the upper Mississippi River near Alton, Illinois. Copeia 1977:166-168.
- THORSON, T. B.
1971. Movement of bull sharks, *Carcharhinus leucas*, between Caribbean Sea and Lake Nicaragua demonstrated by tagging. Copeia 1971:336-338.
1972. The status of the bull shark, *Carcharhinus leucas*, in the Amazon River. Copeia 1972:601-605.

- THORSON, T. B., C. M. COWAN, and D. E. WATSON.
1966. Sharks and sawfish in the Lake Izabal-Rio Dulce system, Guatemala. *Copeia* 1966:620-622.
1973. Body fluid solutes of juveniles and adults of the euryhaline bull shark *Carcharhinus leucas* from freshwater and saline environments. *Physiol. Zool.* 46:29-42.
- THORSON, T. B., and J. W. GERST.
1972. Comparison of some parameters of serum and uterine fluid of pregnant, viviparous sharks (*Carcharhinus leucas*) and serum of their near-term young. *Comp. Biochem. Physiol., Ser. A*, 42:33-40.
- THORSON, T. B., D. E. WATSON, and C. M. COWAN.
1966. The status of the freshwater shark of Lake Nicaragua. *Copeia* 1966:385-402.
- TIBBO, S. N.
1962. New records for occurrence of the white-tip shark, *Pterolamiops longimanus* (Poey), and the dolphin, *Coryphaena hippurus* L., in the northwest Atlantic. *J. Fish. Res. Board Can.* 19:517-518.
- TIBBO, S. N., and R. A. MCKENZIE.
1963. An occurrence of dusky sharks, *Carcharhinus obscurus*, (Lesueur) 1818, in the northwest Atlantic. *J. Fish. Res. Board Can.* 20:1101-1102.
- TORTONESE, E.
1935-36. Pesci del Mar Rosso. *Boll. Mus. Zool. Anat. Comp. R. Univ. Torino*, Ser. 3, 45(63):1-68.
1938. Uno squalo nuovo per il Mediterraneo. *Riv. Sci. Nat. "Natura" Milano* 29:157-160.
1950. Studi sui Plagiostomi. Materiali per una revisione dei *Carcharhinus* Mediterranei. *Boll. Pesca, Piscic. Idrobiol. Roma*, Nuova Ser., 26:5-21.
- 1951a. I. Caratteri biologici del Mediterraneo Orientale e i problemi relativi. *Attual. Zool.* 7:207-251. [Not seen.]
- 1951b. Studi sui Plagiostomi. V-Ulteriori considerazioni sulle specie Mediterranee dei generi *Sphyrna* e *Carcharhinus*. *Doriana* 1(20):1-8.
- URIST, M. R.
1962. Calcium and other ions in blood and skeleton of Nicaraguan freshwater shark. *Science* (Wash., D.C.) 137:984-986.
- VAN HASSELT, J. C.
1823. Uittreksel uit een' brief van Dr J. C. van Hasselt, aan den heer C. J. Temminck. *Alg. Konst-en Lett.-bode* 1(20):315-317.
1824. 73. Sur les poissons de Java. In Le B. de Férussac, Extrait d'une premiere lettre du Dr J. P. van Hasselt à M. C. J. Temminck, p. 89-92. *Bull. Sci. Nat. Géol.* 2.
- WAITE, E. R.
1906. Studies in Australian sharks, No. 3. *Rec. Aust. Mus.* 6:226-229.
1921. Catalogue of the fishes of South Australia. *Rec. S. Aust. Mus.* (Adelaide) 2, 208 p.
- WEBB, P. B., and S. BERTHELOT.
1836-44. Ichthyologie Canarienne. In *Histoire naturelle des Iles Canaries*, Vol. 2, pt. 2, 109 p. Béthune, Paris.
- WHEELER, J. F. G.
1953. In J. F. G. Wheeler and F. D. Ommamey. Report on the Mauritius-Seychelles fisheries survey 1948-1949. *Fish. Publ. Colon. Off.* 1(3):1-145.
1960. Sharks of the western Indian Ocean - III. *Carcharhinus menisorrh* (Müller and Henle). *East Afr. Agric. J.* 24(4):271-273.
1963. Notes on the three common species of sharks in the Mauritius-Seychelles area. *Proc. R. Soc. Arts Sci. Mauritius* 2:146-160.
- WHITE, E. I., D. W. TUCKER, and N. B. MARSHALL.
1961. Proposal to repeal the ruling given in Opinion 47 and to use the plenary powers to stabilize the generic names *Carcharhinus* Blainville, 1816, *Carcharodon* A. Smith, 1838, and *H. dontaspis* J. L. R. Agassiz, 1838, in their accustomed senses (class Pisces). *Z.N.(S.)* 920. *Bull. Zool. Nomencl.* 18:273-280.
- WHITLEY, G. P.
1932. Studies in ichthyology. No. 6. *Rec. Aust. Mus.* 18:321-348.
1934. Notes on some Australian sharks. *Mem. Queensl. Mus.* 10:180-200.
1937. The Middleton and Elizabeth Reefs, South Pacific Ocean. *Aust. Zool.* 8(4):199-273.
1939. Taxonomic notes on sharks and rays. *Aust. Zool.* 9(3): 227-262.
1940. The fishes of Australia. Part 1. The sharks, rays, devil-fish, and other primitive fishes of Australia and New Zealand. *R. Zool. Soc. N. S. W.*, Sydney, 280 p.
1943. Ichthyological descriptions and notes. *Proc. Linn. Soc. N. S. W.* 68:114-144.
1944. New sharks and fishes from Western Australia. *Aust. Zool.* 10(3):252-273.
1945. New sharks and fishes from Western Australia. Part 2. *Aust. Zool.* 11(1):1-42.
1947. New sharks and fishes from Western Australia. Part 3. *Aust. Zool.* 11(2):129-150.
1949. A new shark from Papua. *Proc. R. Zool. Soc. N. S. W.* 1947-48:24.
1950. A new shark from north-western Australia. *West. Aust. Nat.* 2(5):100-105.
- 1951a. Studies in ichthyology No. 15. *Rec. Aust. Mus.* 22:389-408.
- 1951b. Shark attacks in Western Australia. *West. Aust. Nat.* 2(8):185-194.
1964. Fishes from the Coral Sea and Swain Reefs. *Rec. Aust. Mus.* 26:145-195.
1967. Sharks of the Australasian region. *Aust. Zool.* 14(2):173-188.
1968. Some fishes from New South Wales. *Proc. R. Zool. Soc. N. S. W.* 1966-67:32-40.

NOAA TECHNICAL REPORTS

NMFS Circular and Special Scientific Report—Fisheries

Guidelines for Contributors

CONTENTS OF MANUSCRIPT

First page. Give the title (as concise as possible) of the paper and the author's name, and footnote the author's affiliation, mailing address, and ZIP code.

Contents. Contains the text headings and abbreviated figure legends and table headings. Dots should follow each entry and page numbers should be omitted.

Abstract. Not to exceed one double-spaced page. Footnotes and literature citations do not belong in the abstract.

Text. See also Form of the Manuscript below. Follow the *U.S. Government Printing Office Style Manual*, 1973 edition. Fish names, follow the American Fisheries Society Special Publication No. 12, *A List of Common and Scientific Names of Fishes from the United States and Canada*, fourth edition, 1980. Use short, brief, informative headings in place of "Materials and Methods."

Text footnotes. Type on a separate sheet from the text. For unpublished or some processed material, give author, year, title of manuscript, number of pages, and where it is filed—agency and its location.

Personal communications. Cite name in text and footnote. Cite in footnote: John J. Jones, Fishery Biologist, Scripps Institution of Oceanography, La Jolla, CA 92037, pers. commun. 21 May 1977.

Figures. Should be self-explanatory, not requiring reference to the text. All figures should be cited consecutively in the text and their placement, where first mentioned, indicated in the left-hand margin of the manuscript page. Photographs and line drawings should be of "professional" quality—clear and balanced, and can be reduced to 42 picas for page width or to 20 picas for a single-column width, but no more than 57 picas high. Photographs and line drawings should be printed on glossy paper—sharply focused, good contrast. Label each figure. DO NOT SEND original figures to the Scientific Editor; NMFS Scientific Publications Office will request these if they are needed.

Tables. Each table should start on a separate page and should be self-explanatory, not requiring reference to the text. Headings should be short but amply descriptive. Use only horizontal rules. Number table footnotes consecutively across the page from left to right in Arabic numerals; and to avoid confusion with powers, place them to the *left* of the numerals. If the original tables are typed in our format and are clean and legible, these tables will be reproduced as they are. In the text all tables should be cited consecutively and their placement, where first mentioned, indicated in the left-hand margin of the manuscript page.

Acknowledgments. Place at the end of text. Give credit only to those who gave exceptional contributions and *not* to those whose contributions are part of their normal duties.

Literature cited. In text as: Smith and Jones (1977) or (Smith and Jones 1977); if more than one author, list according to years (e.g., Smith 1936; Jones et al. 1975; Doe 1977). All papers referred to in the text should be listed alphabetically by the senior author's surname under the heading "Literature Cited"; only the author's surname and initials are required in the author line. The author is responsible for the accuracy of the literature citations. Abbreviations of names of periodicals and serials should conform to *Biological Abstracts List of Serials with Title Abbreviations*. Format, see recent SSRF or Circular.

Abbreviations and symbols. Common ones, such as mm, m, g, ml, mg, °C (for Celsius), %, ‰, etc., should be used. Abbreviate units of measures only when used with numerals; periods are rarely used in these abbreviations. But periods are used in et al., vs., e.g., i.e., Wash. (WA is used only with ZIP code), etc. Abbreviations are acceptable in tables and figures where there is lack of space.

Measurements. Should be given in metric units. Other equivalent units may be given in parentheses.

FORM OF THE MANUSCRIPT

Original of the manuscript should be typed double-spaced on white bond paper. Triple space above headings. Send good duplicated copies of manuscript rather than carbon copies. The sequence of the material should be:

FIRST PAGE

CONTENTS

ABSTRACT

TEXT

LITERATURE CITED

TEXT FOOTNOTES

APPENDIX

TABLES (provide headings, including "Table" and Arabic numeral, e.g., Table 1.--, Table 2.--, etc.)

LIST OF FIGURE LEGENDS (entire legend, including "Figure" and Arabic numeral, e.g., Figure 1.--, Figure 2.--, etc.)

FIGURES

ADDITIONAL INFORMATION

Send ribbon copy and two duplicated copies of the manuscript to:

Dr. Carl J. Sindermann, Scientific Editor
Northeast Fisheries Center Sandy Hook Laboratory
National Marine Fisheries Service, NOAA
Highlands, NJ 07732

Copies. Fifty copies will be supplied to the senior author and 100 to his organization free of charge.